



सत्यमेव जयते

INDIAN AGRICULTURAL  
RESEARCH INSTITUTE, NEW DELHI

I.A.R I.6.

GIP NLK—H-3 I.A.R.1.—10.5.55—15,000

50217

HISTORICAL ASPECTS OF  
ORGANIC EVOLUTION



# HISTORICAL ASPECTS OF ORGANIC EVOLUTION

by

PHILIP G. FOTHERGILL,  
B.Sc., Ph.D.

*Lecturer in Botany, King's College, University of Durham,  
Newcastle upon Tyne: one time Joint Secretary of the University of  
Durham Schools Examination Board.*

With a Foreword

by

J. W. HESLOP HARRISON,  
D.Sc., F.R.S., F.R.S.E.

50279



IARI

50279



LONDON  
HOLLIS AND CARTER

1952



MADE AND PRINTED IN GREAT BRITAIN  
BY CHARLES BIRCHALL AND SONS, LTD.,  
FOR HOLLIS AND CARTER LTD.  
25 ASHLEY PLACE, LONDON, S.W.1

*First published 1952*

*To*  
*My Parents*  
*and*  
*J. W. H. H.*



## FOREWORD

NO DOUBT there is an abundance of literature dealing with the subject of evolution but, in writing this book Dr. Fothergill has had three special objects in mind: (1) to fill gaps in the literature in respect to the history of the subject and to bring this aspect of the subject up to date, (2) to present it in such a manner as to enable both the general and specialist reader to evaluate the conflicting meanings that have been applied to the word "evolution", (3) by presenting an unbiased account of the subject of evolution to show that even a person believing in a definite and clear-cut religion can also believe in and deal with the subject of evolution without prejudice to his religious beliefs.

Except for Clodd's more or less biased *Pioneers of Evolution* little has been published in England concerning the history of one of the most important developments in biological thought, although Henry Fairfield Osborn's book *From the Greeks to Darwin* has been available to students on both sides of the Atlantic. Under these circumstances it seemed imperative that some one in this country should attempt a new study of the history of evolution in such a way as to bring our knowledge of that aspect of the subject into line with the general conceptions of evolution as built up in the many excellent textbooks which have been produced recently. The special merit of this book is that, by the method of treatment of evolution, it attempts to show that the concept is not necessarily materialistic.

As a result of his own experience as a practical teacher of biological sciences, including that of evolution, Dr. Fothergill had early recognised the difficulties encountered in teaching the development of evolutionary views throughout the ages without the aid of a really satisfactory book. To remedy that defect he began to investigate the matter from the historical point of view and the results are embodied in the present study. In my opinion, in his self-imposed task, which most biological research investigators would have shirked, Dr. Fothergill has attained a very considerable measure of success in securing the three objects he had in mind.

It is my sincere hope that Dr. Fothergill's labours will reap the rewards and gain the recognition they so well deserve.

J. W. HESLOP HARRISON,  
D.Sc., F.R.S., F.R.S.E.

Newcastle upon Tyne,  
January, 1951.

*“ He who looks not back loses his way ”*  
(an old Indian proverb)

*“ All men desire by nature to know ”*  
(Aristotle)

*“ The analytical reasoning of the new scholasticism is valid within its own field, even though the senses, visus, tactus, gustus, offer no more verification than they did to the older scholasticism, whose deductive reasoning was also right in many of its conclusions about invisible values and realities of another and a higher order. There is no real contradiction between the valid results of analytical science, and the valid results of synthetic philosophy.”*

(Alfred Noyes:  
*The Unknown God*)

*“ Melior est causa causæ quam causa causati ”*

## CONTENTS

FOREWORD .. .. .	Page vii
INTRODUCTION .. .. .	xv

## PART I

### HISTORICAL DEVELOPMENT OF THE IDEA OF ORGANIC EVOLUTION

#### CHAPTER 1. THE EARLY PERIOD

1.	Introduction .. .. .	3
2.	Historical Formulation .. .. .	7
3.	<i>The Obscure Period: Ancient Chinese, Babylonian and Egyptian Thought</i> .. .. .	9
4.	<i>The Greek and Medieval Period</i> .. .. .	11
	(a) <i>The Early Ionians</i> .. .. .	12
	(b) <i>The Later Ionians</i> .. .. .	14
5.	<i>Aristotle</i> .. .. .	18
	(a) <i>General Account</i> .. .. .	18
	(b) <i>Biology of Aristotle</i> .. .. .	21
	(c) <i>Aristotle and Evolution</i> .. .. .	25
6.	<i>The Post-Aristotelians</i> .. .. .	33

#### CHAPTER 2. THE SPECULATIVE PERIOD UP TO 1790 A.D.

1.	The Early Classifiers .. .. .	37
2.	Seventeenth and Eighteenth Century Contributions .. .. .	37
	(a) <i>The Naturalists</i> .. .. .	38
	(b) <i>The Speculative Philosophers</i> .. .. .	44
	(c) <i>George Louis Leclerc Buffon</i> .. .. .	47
	(d) <i>The Natural Philosophers</i> .. .. .	51

# CHAPTER 3. THE PERIOD OF FORMULATION Page FROM 1790 TO 1900

## (A) THE REAL BEGINNINGS OF EVOLUTIONARY THEORY

1. *Introduction : The Revolt against Mediæval Philosophy* .. 59
2. *Erasmus Darwin* .. .. . 62
3. *Lamarck and Lamarckism* .. .. . 68

# CHAPTER 4. THE FORMULATIVE PERIOD CON- TINUED

## (B) FURTHER DEVELOPMENTS AND SOME SIDE ISSUES

1. *The Growth of Ideas in Biology* .. .. . 79
2. *Transformation immediately following Lamarck* .. .. 81
  - (a) *Johann Wolfgang von Goethe* .. .. . 81
  - (b) *James Cowles Prichard* .. .. . 83
3. *Baron Cuvier* .. .. . 86
4. *Cuvier's Contemporaries* .. .. . 90
5. *Richard Owen* .. .. . 92
6. *Palæontology* .. .. . 97
7. *The Cell Theory* .. .. . 100
  - (a) *The Groundwork of the Theory* .. .. . 100
  - (b) *The Formulation of the Theory by Schleiden and Schwann* .. .. . 101

# CHAPTER 5. THE FORMULATIVE PERIOD CON- TINUED

## (C) CHARLES DARWIN AND DARWINISM

1. *Introduction* .. .. . 104
2. *Charles Darwin and "The Origin of Species"* .. .. 106
3. *Darwin's Theory* .. .. . 111
  - (a) *Variation* .. .. . 111
  - (b) *Overproduction and the Struggle for Existence* .. 112
  - (c) *Natural Selection* .. .. . 113
4. *The Reception of Darwinism* .. .. . 115
5. *Contemporary Criticisms of Darwinism* .. .. . 122
  - (a) *Mivart's "The Genesis of Species"* .. .. . 122
  - (b) *Mivart on Evolution and Religion* .. .. . 128
  - (c) *Jenkins' Criticism* .. .. . 132
  - (d) *Korschinsky's Criticisms* .. .. . 133

## CHAPTER 6. THE FORMULATIVE PERIOD CON- Page CLUDED

### (D) AFTER DARWIN

1.	<i>The Establishment of Evolution as a Principle</i>	..	..	135
	(a) <i>General Effects</i>	..	..	135
	(b) <i>Neo-Darwinism and Neo-Lamarckism</i>	..	..	138
2.	<i>Alfred Russel Wallace</i>	..	..	140
3.	<i>Theories supplementary to Natural Selection</i>	..	..	143
	(a) <i>The Theory of Sexual Selection</i>	..	..	143
	(b) <i>Isolation Theories</i>	..	..	145
	(c) <i>Roux's "Battle of the Parts"</i>	..	..	150
	(d) <i>Organic Selection</i>	..	..	151
	(e) <i>Weismannism</i>	..	..	152
4.	<i>Theories replacing Natural Selection</i>	..	..	160
	(a) <i>The New Lamarckism</i>	..	..	160
	(b) <i>Orthogenesis</i>	..	..	166
	(c) <i>Heterogenesis</i>	..	..	170

## PART II

## CYTOGENETICS AND THE MODERN CAUSAL THEORIES OF ORGANIC EVOLUTION

### CHAPTER 7. THE MODERN PERIOD FROM 1901

#### (A) THE TURNING POINT IN EVOLUTIONARY THEORY

1.	<i>Introduction</i>	..	..	..	..	181
2.	<i>Genetics</i>	..	..	..	..	182
	(a) <i>The Advent of Mendelism</i>	..	..	..	..	182
	(b) <i>The Cytological Explanation of Mendelism</i>	..	..	..	..	186
	(c) <i>Pure Line Theory</i>	..	..	..	..	189
3.	<i>Chromosomes as Aids in Species Determination</i>	..	..	..	..	190
4.	<i>Cytogenetics</i>	..	..	..	..	193
	(a) <i>Deviations from Mendelian Expectations</i>	..	..	..	..	193
	(b) <i>The Chromosomes as Bearers of the Genes or Factors</i>	..	..	..	..	197
	(c) <i>Cytological Evidence for the Chromosome Theory of Heredity</i>	..	..	..	..	201



	Page
<b>CHAPTER 8. THE MODERN PERIOD CONTINUED</b>	
<b>(B) CYTOGENETICS AND EVOLUTION</b>	
1. <i>Introduction</i> .. .. .	212
2. <i>Variation</i> .. .. .	214
3. <i>Chromosomal Changes</i> .. .. .	216
(a) <i>Changes involving whole Sets of Chromosomes</i> ..	216
(b) <i>Individual Chromosomal Aberrations</i> ..	224
4. <i>Internal Chromosomal Arrangements</i> .. ..	225
(a) <i>Deficiencies and Deletions</i> .. ..	227
(b) <i>Duplications</i> .. .. .	227
(c) <i>Translocations</i> .. .. .	228
(d) <i>Inversions</i> .. .. .	233
5. <i>The Ultimate Unit of the Chromosome</i> .. ..	235
(a) <i>The Gene: General Features</i> .. ..	235
(b) <i>The Chemical Nature and Function of Genes</i> ..	238
6. <i>Criticisms of the Gene Theory and of the Chromosome</i> <i>Theory</i> .... .. .	241
(a) <i>Introduction and General Criticisms</i> ..	241
(b) <i>Special Criticisms</i> .. .. .	244
<b>CHAPTER 9. THE MODERN PERIOD CONTINUED</b>	
<b>(C) MODERN CAUSAL THEORIES OF EVOLUTION</b>	
1. <i>Neo-Lamarckian Ideas</i> .. .. .	251
(a) <i>General Account</i> .. .. .	251
(b) <i>Modern Evidence in Support of Lamarckism</i> ..	253
2. <i>Biomechanical Evolution formulated through Orthogenetic</i> <i>Phenomena: Aristogenesis</i> .. .. .	274
3. <i>Lotsy's Theory of Evolution by Means of Hybridization</i> ..	280
4. <i>Willis' Theory of Evolution by Means of Divergent</i> <i>Mutation</i> .. .. .	283
(a) <i>The Age and Area Theory</i> .. .. .	283
(b) <i>Evolution by Differentiation or Divergent</i> <i>Mutation</i> .. .. .	285
5. <i>Goldschmidt's Ideas of Micro- and Macro-evolution</i> ..	288

## CHAPTER 10. THE MODERN PERIOD CONCLUDED

## (D) MODERN NEO-DARWINISM : MUTATIONS AND SELECTION

1.	<i>The Induction of Mutations</i>	..	..	..	..	296
	(a) <i>Mutations Induced by Chemical Means</i>	..	..	..	..	298
	(b) <i>Mutations induced by Heat</i>	..	..	..	..	302
	(c) <i>Mutations induced by Short Wave Radiations</i>	..	..	..	..	304
2.	<i>Gene or Point Mutations</i>	..	..	..	..	310
3.	<i>Natural Selection</i>	..	..	..	..	319
	(a) <i>General Account</i>	..	..	..	..	319
	(b) <i>Evidence for the Occurrence of Natural Selection</i>	..	..	..	..	322
	(c) <i>Natural Selection and Evolution</i>	..	..	..	..	339

EPILOGUE	..	..	..	..	..	..	342
----------	----	----	----	----	----	----	-----

## APPENDICES

1.	<i>Aristotle's Theory of Matter and Form</i>	..	..	..	..	351
2.	<i>Aristotle's Classification of Animals</i>	..	..	..	..	352
3.	<i>A Synopsis of Lamarck's Classification of Animals</i>	..	..	..	..	358
4.	<i>A Factorial Account of One of Mendel's Experiments</i>	..	..	..	..	360
5.	<i>Examples of Genetical Experiments and Applications</i> <i>worked out Statistically</i>	..	..	..	..	363
6.	<i>Some further Lamarckian Experiments</i>	..	..	..	..	368
7.	<i>An Account of Muller's Technique for recognising Mutations and for measuring the Mutation Rate</i>	..	..	..	..	371
8.	<i>A Synopsis of, and reference to, the earlier Experiments demonstrating the occurrence of Natural Selection</i>	..	..	..	..	377

BIBLIOGRAPHY	..	..	..	..	..	..	379
--------------	----	----	----	----	----	----	-----

PUBLICATIONS	..	..	..	..	..	..	383
--------------	----	----	----	----	----	----	-----

INDEX	..	..	..	..	..	..	409
-------	----	----	----	----	----	----	-----



## INTRODUCTION

ALTHOUGH it has become customary to apologise for the appearance of books on Evolution, I make no apology for this one. I feel that there is a need for an up-to-date historical book of this type. The idea of evolution is probably as old as the grass on the hillsides, and is not in any way dependent on any particular causal theory of evolution. Nothing seems to be more certain than that our ideas about this concept which we call "evolution" will be supplanted by a much more accurate one in future years. I believe, too, that the historical approach (which is looked down upon by so many people) is, first, the surest guide to an insight into the minds of the great men who have been and who are concerned with such concepts as those of evolution, and, secondly, the correct approach if we desire to obtain an idea of the true value and meaning of the concept of evolution in the biological world. I hope, therefore, that this book will appeal to all students of biology.

There is a short history attached to the motive which impelled me to write on this topic. May I begin by thanking my teacher and friend, Professor J. W. Heslop Harrison, D.Sc., F.R.S., F.R.S.E., that inimitable man whose personality spreads like a warm glow on a winter's evening over all who come in contact with him! He it was who first showed me some of the secrets of evolution and first opened my eyes to the attractive vista of the evolutionary field. But, he did more than this, for his methods taught me to look at things confidently but critically.

Later I started a controversy on "Evolution" in the columns of the *Catholic Herald* which lasted for six months or so. I owe a debt of gratitude to the editor of this journal, Count Michael de la Bedoyere, for encouraging the controversy. In the controversy I appealed for tolerance and openmindedness among Catholics. The experience I gained was large and it taught me that many people, including some Catholics, had a tendency to look at the scientific doctrine of evolution in the wrong way. I became aware that there were many people who thought that one could look at the scientific theory of evolution from a Catholic, or a Protestant, or a Buddhist, *point of view*. The conviction grew in my mind that an historical book on the subject would do much good, and was confirmed when I discovered that my publishers, particularly Mr.

Douglas Jerrold and Mr. Christopher Hollis, thought likewise. The writer is a Catholic, but one of the aims of the book is to show that any person holding any form of religious belief is quite able to write and expound a scientific theory on a purely phenomenal and evidential level. And so this small effort came to be written, but not without some considerable difficulties due to war circumstances and illnesses.

The book is divided into two parts. Part One deals with the early history of the development of the idea of organic evolution; the subject matter is treated chronologically, and takes the study of evolution up to about 1900 A.D., when the modern genetical era may be said to have started. In very early times there was really no conception of evolution. But in the biological and philosophical notions of those days clues to the evolution of the idea of evolution may be discerned. We have attempted to find these clues, and hence this part of the story deals in large measure with biological and philosophical notions which may lead to clues pointing the way to the strictly evolutionary story given later in the book. In Part Two the style of the book changes. The chief reason for this is that, in the author's opinion, modern evolutionary ideas cover so vast a field as to make their chronological treatment confusing and unpractical. Part Two, then, deals with the chief modern causal theories of evolution and their relationship to formal genetics. A fairly detailed account of cytogenetics has been given to enable those readers who are not specialists to understand the relationship between evolution and genetics. There is a comprehensive bibliography and an appendix, permitting those readers who wish to pursue certain topics further to do so.

Throughout the book the author has attempted to keep his own personal opinions in the background and to keep personal criticism to the absolute minimum. In a book such as this, however, a certain amount of personal bias is bound to creep in, but the author here begs the indulgence of his readers and critics, knowing well enough that they also will be biased to some extent. The epilogue gives a cursory summing-up, and here the author has allowed his personal feelings about evolution to come to the surface.

This book, then, deliberately covers a very wide field, and no man can pretend to be master of them all. Mistakes are thus inevitable, and for all of these I apologise beforehand. If I have unwittingly stated the evolutionary viewpoint of a living author wrongly, I apologise for this, too, and hope to be corrected.

Because of the scope of this book it is hoped that it will appeal to a wide public, some of whom may be interested in all of the subject matter, others may only be interested in more specialist parts of the book. The book is offered to intelligent laymen interested in evolutionary biology, to teachers of various kinds, to students and to the professional biological public in the hope that it may help them to form a balanced opinion on the subject of "Evolution". Considering the complexities of the subject and the ground covered, I hope that professional biologists will find it not unreasonable in outlook.

I would like to thank my publishers, who readily agreed to all suggestions, and also to the writers of the many books and papers which I have used or from which I have quoted. It is impossible to mention them all, but they are all acknowledged in the text, in footnotes, and in the bibliography. In particular, I wish to thank the publishers of *Biology*, who allowed me to reprint most of an article of my own on "Experimental Genetics in Schools". I would like to acknowledge my indebtedness to my colleague, the late Mr. G. N. Robinson, B.Sc., who helped me in writing the section on the "Chemical Nature of the Gene", to my friend Dom Benedict Crook, O.S.B., M.A., who corrected the manuscript of the first five chapters, and to the Rev. A. M. Young, O.S.B., of Douai Abbey, who helped me over some difficulties with Kant and the other Natural Philosophers, to my colleagues Dr. Eveline Elliot, who went through all the proofs, and Dr. Ursula Philip, who made constructive suggestions on the treatment of genetics in the appendix. Most of all, however, I find it impossible to express my gratitude to Professor M. Thomas, M.A., F.R.S., F.R.S.E., who went through the whole of the text word for word, and but for whose painstaking labours the book would probably never have been completed. I would like to thank Mr. P. Gibson, of the Department of Botany, King's College, who executed all the line drawings. The quiet pervading influence of my wife Ethel, in spite of many domestic vicissitudes, has also helped me out of many difficulties. I beg to acknowledge the receipt of a research grant from the Research Committee of King's College, Newcastle upon Tyne, which defrayed some of the expenses of the book.

*King's College, Newcastle upon Tyne, 2.*

*January, 1951.*



## PART I

# HISTORICAL DEVELOPMENT OF THE IDEA OF ORGANIC EVOLUTION





## CHAPTER I

### THE EARLY PERIOD

#### I. INTRODUCTION

**E**VEN the most mundane man, provided he is intelligent, must have at times thought about himself in a detached kind of way. He must have wondered what relation he bears to other men, to other creatures, to the world and to the universe. He must have wondered what life is, where it came from and how it arose. Many men, not finding any solution to these perplexing problems, have dropped the matter and have returned to their daily tasks, still conscious, no doubt, of an air of mystery around a matter which should be solved because it so intimately concerns each and every one of us. Other men, however, being more or less consciously philosophical in outlook, probers who refuse to take *no* for an answer, have not ceased their enquiries just when the problems were becoming most fascinating and interesting, just when their solution seemed most vital and needful. The theory of evolution attempts to solve some of these problems, and thus it is true to say that evolution, in a wide sense, is an idea belonging to all historical ages.

Thus almost from the earliest times of which we have any written records, we find that these eternal problems of life, its origin and mode of progression have engaged the thoughts of men. The early history of evolution begins in mythology and can scarcely be separated from it. Gradually there emerged from the mists of these phantasies a conscious appreciation of life and all that it means treated in a naturistic way. Finally we come to the modern era of evolution. In point of fact, it was in the nineteenth century that evolution as a definite conception first became a topic of serious *scientific* discussion.

In discussing a theory such as that of evolution, treated in a general way, and looked at from various angles, it is not likely that any one person would be found who is a specialist in all branches of knowledge which will be touched upon. In the modern world a person can only be a specialist in one, or at most a few, branches

of knowledge. Over-specialisation may be a modern necessity but it brings its own dangers. For specialists are often so engrossed in their own narrow line of enquiry that they lose their perspective, and their outlook on the whole subject sometimes tends to become warped. Such a person is the last one capable of giving information of general value unless he makes full use of the works of other writers. Many people are unfortunately narrow minded enough to insist that a person of scientific training should confine himself to topics which are strictly scientific and should not delve into philosophy, or related subjects, because he lacks a training in the method of approach to them. The writer on general subjects touching both science and philosophy could not answer this objection better than by quoting a theologian, the Very Rev. Dr. C. L. Souvay,<sup>1</sup> who, when discussing these very matters, says "while this is true, still need one be a past master in all branches of knowledge in order to be permitted to give an opinion on one of them? And will a scientist be accused of poaching upon the other man's preserves if he wishes to exercise his God-given right to philosophise? Of course not. Only let him remember, first to observe scrupulously the rules of the game; and second, that on this subject he is but a dilettante—." An admonition of this kind, of course, applies equally to anyone commenting from his point of view on any subject in which he has not been specially trained.

The topics discussed in this book will be numerous and will embrace several branches of both science and philosophy. Our task is to bring together information obtained from many sources, in an attempt to trace the development of the idea of evolution as it is applied to living things. Full use therefore will be made of quotations.

There is a common lay opinion that Darwin, or perhaps Lamarck, was the first person to conceive the idea of evolution. The violent scientific controversies of the latter half of the last century have probably helped to strengthen this view. Darwin, however, was the first to enunciate the principle of descent with *modification* brought about by fortuitous and natural means. His predecessors, for the most part, failed to appreciate this aspect of nature. They knew of variations among living things and related organisms; they knew of sports (or mutations as we call them nowadays); they believed in inheritance; and it has been said that a dim appreciation of natural selection was expressed over two thousand years before

<sup>1</sup> In *Messenger*, 1931, p. xvii.

the time of Darwin. But it was Darwin's genius for grasping a multitude of small facts that enabled him to synthesise previous knowledge of the subject into a single system (descent with modification). The scientific theory of organic evolution was thus definitely formulated and made coherent, but Darwin was not the first to think of the idea of evolution. Darwin's theory was apparently confirmed by a large mass of observational facts. As time went by the number of observations and even the experimental evidence increased enormously and tended to establish the theory on a firm basis. So also there was an increase in the number of observations and in experimental matter which raised difficulties for the theory—difficulties which enthusiasts of this theory of evolution often overlook.

It should be obvious that neither Darwin nor Lamarck, nor any other single person, discovered evolution. Many previous writers, often philosophers or theologians, had had glimpses of the idea. Many of the earlier botanists and zoologists strove to classify things. Whether or not their classifications were really *natural* matters little from an historical point of view, for all such systems imply *some* sort of relationship between the things classified. This relationship may be a purely mental one, or it may purport to be truly phylogenetic. Some people may scorn the efforts of these earlier evolutionists and systematists; they, however, did their work well and each advanced his science a little.

At first, species were considered to be immutable, then it came to be realised that they could change (or evolve); later the species were thought to be so related to each other as to form a kind of phylogenetic tree with a central trunk and innumerable subsidiary branches. Some of the side branches of this tree, which represented lines of evolution of small groups of species, were sometimes purely imaginary. Some modern orthogeneticists consider that species, or at least groups of species, have evolved in parallel lines, each line remaining separate throughout millions of years, stretching far back into the almost immeasurable past to the beginnings of living things. From a pantheistic conception arose a theistic conception, which in turn gave place to the idea of a definite personal Creator creating each species separately. This provoked a violent materialistic reaction. But what is the modern conception of evolution by parallel lines if not a modification of the theory of special creation?

In a few hundred or a thousand years time the biologists of the

period may laugh at our puny attempts to unravel nature's ways. For one thing seems certain, and that is, that the evolutionary theory of that time will bear as little resemblance to our twentieth-century theory as ours bears to that of the early Greek philosophers, or as modern theoretical atomic physics bears to the atomism of Democritus, or even to Dalton's theory.

There is, in fact, an evolution of the idea of evolution and the moral of all this is that no real scientific principle arises spontaneously in one man's mind. All our ideas are dependent on the development of ideas put forward in previous centuries. As Osborn<sup>1</sup> says: "yet the conviction grows with enquiry that the Evolution law was reached not by any decided leap, but by the progressive development of every subordinate idea connected with it, until it was recognised as a whole by Lamarck, and later by Darwin". It behoves us then to consider the history of our subject in some detail as a fitting introduction to the other biological topics. The study of the history of a subject is a great mental discipline; it teaches us humility and shows us our faults. Unfortunately, many modern scientific persons scorn history of any sort, and refuse to learn its lessons, for in their pride they think that, because of modern developments, their minds are above the writings of the great thinkers of the past. History to such people is merely a series of dates. But they forget that dates are only milestones, as it were, pointing out the path of true knowledge. It is the space between the milestones which is interesting. If then we can give a connected account of the history of the idea of evolution, utilising both milestones and the path between them, we may do some good.

There are only a few comprehensive English textbooks on the History of Evolution to which the general reader, or even the specialist, could go for full information. We owe a great deal to Prof. H. F. Osborn<sup>2</sup> for his well constructed book *From The Greeks To Darwin* and to the Rev. Dr. E. C. Messenger<sup>3</sup> for his classic *Evolution and Theology*, and also to C. Singcr<sup>4</sup> and Nordenskiöld<sup>5</sup> and some others. A large amount of information on the subject can be gleaned from numerous articles and papers in a variety of books and journals.

<sup>1</sup> 1924, p. 2.

<sup>2</sup> 1924.

<sup>3</sup> 1931.

<sup>4</sup> 1921, 1941.

<sup>5</sup> 1929.

## 2. HISTORICAL FORMULATION

Man's observation of nature began from the earliest times; evidence of this is to be found in the drawings of bisons and other animals on the walls of caves used by prehistoric man of the Stone Age and later. Often these drawings were beautifully executed but they scarcely indicate a knowledge of biology. Prehistoric man was forced to hunt and slay such creatures for food. Thus he soon learnt the position of the most vulnerable part of an animal, namely the heart region. The earliest men were probably forest dwellers not because, as some imagine, they had just descended from some simian-like creature, but because in these early times there were few of them. Hence the forest, especially the thick tropical or semi-tropical forest, provided abundant and easily obtainable food, while at the same time affording the maximum of naturally occurring protection against a multitude of enemies. Later, man became nomadic, roaming around, seeking the best and safest places. Gradually, however, as families and clans increased in number, he learnt the benefits of settling down on, or near to, grassland where he could keep his own cattle and grow his own crops. The earliest biology was then undoubtedly of a practical nature—agriculture. The earliest civilizations were probably also grassland civilizations. And this condition has persisted right up to the present day; too often are we prone to forget the debt we owe to grass. This age is just as much the grass age as it is the steel age, or the age of aeroplanes, or of atomic bombs.

After this short digression let us return to the topic of our chapter. It is generally assumed that the history of evolution begins with the Greeks. Osborn,<sup>1</sup> for instance, finds that there are two major periods in the history of Evolution to be considered; (a) the Anticipation of Nature: Greek Evolution from 640 B.C. to 1600 A.D., and (b) the Interpretation of Nature: Modern Evolution from 1600 A.D., to the present day. On the other hand Coulter<sup>2</sup> considers that there have been three chief periods which are based on the method of attacking the problems of the subject. These are:—(a) the Period of Speculation beginning with the earliest Greek thinkers and extending up to 1790. Up to this time all writings upon evolution were purely speculative, no experimental matter and few real observations were offered to support the ideas of the writers;

<sup>1</sup> 1924, pp. 10-11.

<sup>2</sup> 1926, p. 488.

(b) the Period of Observation and Inference extending from 1790 A.D. up to 1900 A.D. In the earlier period species were thought to be immutable, but with the increase in knowledge about natural creatures brought about by the birth of anatomy, ecology and other special branches of biology, it gradually became evident that this was not true. Geology became a science and gradually evolution progressed from an *idea* to a *principle*, and so the second period was ushered in. In this period which started with Goethe, St. Hilaire and Erasmus Darwin, the assumption was made that mere external resemblance of species showed some degree of relationship. Obviously an assumption of this kind enabled one to draw inferences of far-reaching importance. The outstanding figure of this period was Charles Darwin, who, says Coulter,<sup>1</sup> "carried the method to the limits of its possibilities, observing through several years a world-wide range of forms in connection with the famous voyage of the *Beagle*". (c) Coulter's third period is the Time of Experimentation beginning in 1900 and extending to the present day. This period would probably have begun with Mendel had his classic work on garden peas been appreciated at the time. But, like all who are before their time, Mendel's work suffered eclipse and it was relegated to the files of obscurity for well-nigh half a century. Thus it was that the period of experimentation began with De Vries, who, along with Correns and Tschermak, rediscovered Mendel's principles and actual writings, and who later brought forth his own ideas of mutation. At the present time experimental evolution is bound up with the science of genetics. The number of actual experiments which have been carried out bearing on evolution as distinct from heredity is, however, very small indeed.

It is clear then that evolution as a definite, seriously considered, scientific principle first took definite shape in the second half of the nineteenth century. Since then great strides have been made in collecting facts and figures which bear on the theory, but so far there is no satisfactory philosophical account of the true meaning of the principles of evolution. Probably no fundamental vital idea has yet emerged which is not to some extent a rehash, or re-interpretation, of mediæval or earlier thought on the subject.

It is convenient for our purpose then to divide the history of evolution into five periods as follows :—

- (a) The Obscure Period,
- (b) The Greek and Mediæval Period,

<sup>1</sup> 1926, p. 489.

- (c) The later Speculative Period up to about 1790 A.D.,
- (d) The Period of Formulation from 1790 to about 1900 A.D.,
- (e) The modern Synthetic or Genetical Period, attacking the problems of the cause of evolution.

### 3. THE OBSCURE PERIOD: ANCIENT CHINESE, BABYLONIAN AND EGYPTIAN THOUGHT

Unfortunately there is very little record and no extant continuous account at all of the development of the biological ideas of the ancient Chinese, Babylonian and Egyptian cultures. The marvellous civilizations of the East have left few traces of their scientific thought. The Greeks were the first to give distinct accounts of nature so far as we know. They regarded science as a branch of philosophy, and in fact they did not discern between the two. Thus it is that the history of biology and its branches and of science in general is usually regarded as beginning with the Ancient Greeks, or Greek-speaking peoples, about six centuries before Christ.

It is not quite accurate, however, to assert categorically that the Greek philosophers were the first, or only, ancient thinkers who discovered the ideas of evolution. The Chinese culture is one of the most ancient of all, but, naturally enough, due to language difficulties, it is probably little known or appreciated in the western world. Burnet<sup>1</sup> reminds us that though the material civilization may pass easily from one race of people to another in spite of language difficulties, this cannot be the case with philosophical notions on account of their very nature, as knowledge of the language is essential for their proper understanding.

Some of the very ancient writings of the early Chinese philosophers have been investigated from the point of view of the origin of life and its evolution by Dr. Tye Tuan Chen.<sup>2</sup> He tells us that the Chinese conceived that only five primary elements existed at the beginning of the world. These were, water, wood, fire, soil and the precious metal gold. It was thought that life arose through the positive and negative interactions of these primitive stuffs. To express what we mean by evolution the Confucians used the word *Ti* and the Taoists used *Tao*. In their philosophy, then, both the early Confucians and the Taoists may have appreciated

<sup>1</sup> 1930, p. 17.

<sup>2</sup> 1929.



at least the fundamental meaning behind the idea of evolution. To them, *Yi*, or *Tao*, meant some kind of change in the natural world—a change from simple to complex. As early as the sixth century before Christ, Confucius in his *Yi-Chang* tried to show that “complexity was derived from a single source” and that “things were originated from a single simple source through gradual unfolding and branching”.<sup>1</sup> Chen also found that many of these thinkers at least appreciated, or recognised, what we now call variation, adaptation and the idea that structure and function are interrelated. There are many recognisable points of connection between these early ideas and those of the various early Greek schools of thought. For instance, the existence of primary elements was upheld by both cultures; Empedocles and Aristotle recognised four, whereas the Chinese knew five. We notice that among the Chinese primary elements are wood and gold which are both substances of great value and utility. The primary elements of the Greeks, on the other hand, can be considered more as abstractions than substances; at least they did not correspond to what we understand by the same terms today. Adaptation and like ideas were also known to Aristotle. In some respects the evolutionary ideas of the Chinese would seem to be in advance of those of the Greeks.

The Egyptians especially certainly had a knowledge of the medicinal properties of plants. As Slaley<sup>2</sup> tells us, much of their biological knowledge was in the form of farm-lore and dealt with food recipes for cattle and poultry and the diseases of animals. G. J. Dudycha<sup>3</sup> says “The Greeks were not the first to speculate concerning the origin of things, for we find among the Egyptians and the Babylonians cosmogenic ideas of far more ancient origin, which, when divested of their theological implications and deity names, are not so far different in nature and significance from those of more recent and of western thought”. Many of these cosmogenic ideas are to be found in the *Legend of the Creation*. A copy of the original of this, dating from about 311 B.C., is to be found in the British Museum. The original itself has never been found. Dudycha amplifies a translation of this copy which was made by Dr. Budge.<sup>4</sup> *Neb-er-tcher* in the form of *Khepera* is the creator of all. *Nu* is the abyss of water out of which *Khepera* raised all things to

<sup>1</sup> 1929, p. 50.

<sup>2</sup> 1942.

<sup>3</sup> 1932, p. 269.

<sup>4</sup> 1912.

life. Previous to this apparently they lay in a state of inertness. The origin of man is described in the section called the *Vision of Hermes* as the becoming actual from the mind of *Neb-er-cher* through seven distinct stages before the soul of man is recognisable as human.

From the point of view of cosmic evolution the chief things to notice in these writings are (a) a Divine Intelligence and Creator, (b) water as a primitive and boundless substance, (c) the potentiality of all things in the Divine Intelligence and (d) creation as the process of becoming actual by stages. As Dudycha<sup>1</sup> points out, this creation by *Khepera* and the development of man represent both an evolutionary, or unfolding, process and an epigenetic, or building up, process. "These two are not incompatible, for the souls although passing through an epigenetic process towards materiality are the unfoldment of that which is in Divine Intelligence".

As we have already noted in connection with the writings of the early Chinese philosophers, so we also find that many of the ideas of the Ancient Egyptians are found in later Greek writings, and even in those of early Christians and of the Fathers of the Church. The Ionian Thales also taught that water was the primordial element. The state of inertness in which things lay according to the Egyptians may correspond to the potentiality of creation and evolution as held by St. Augustine. According to him, the fiat of the Supreme Intelligence was necessary to set the unfolding process in motion whereby the potential and inert became actual.

Finally, as regards the scientific opinions of the Babylonians, we find that little is known about the state of their science, because so few of their writings have come down to us. From the scanty material available it is possible to say that they seem to have emphasised the importance of the magical or mystical powers pervading the universe. Nevertheless, they developed the science of medicine to a fairly high degree and Nordenskiöld<sup>2</sup> tells us that their knowledge of the higher animals was considerable. But we know nothing of their actual evolutionary views.

#### 4. THE GREEK AND MEDIAEVAL PERIOD

This period begins with the Ionian School of Philosophy at Miletos in the sixth century before Christ. The Ionians were

<sup>1</sup> 1932, p. 267.

<sup>2</sup> 1929, p. 6.

Grecian immigrants to the Aegian Islands: thus they lived near to the Persian Empire and were not a great distance away from Egypt. Hence their geographical position was central and they took advantage of this, for they were essentially travellers and merchants. It is probable that they, and their Grecian successors, knew, if not by actual written records, at least by tradition, of the scientific legacy of the more ancient Chinese, Persian and Babylonian civilizations. Many of them certainly visited Egypt, where they became acquainted with science and mathematics which they later developed. The Greeks, in fact, did not hesitate to acknowledge their debt to other traditions and peoples. R. W. Slaley<sup>1</sup> tells us that "through the Greeks the legacy of Egypt was transmitted to the rest of the world".

In this connection of transmission of ideas from one people to another, we must remember that while language differences would render it difficult to pass on involved philosophical ideas, scientific and medical matters would, in all probability, soon be broadcast among peoples of neighbouring regions.

The Ionian school of philosophy may be divided into two groups, (a) the Early Ionians, and (b) the Later Ionians. It is necessary now to consider some of their general ideas to see whether we can discern any evolutionary leanings.

#### (a) *The Early Ionians*

Our information about these philosophers is dependent to a very great extent on the remarks of the later writers, like Heraclitus and Aristotle. The written material they have left behind is scanty. It is difficult to tell, even from Aristotle's account of them, whether they were theists or pantheists. They are sometimes called dynamists because they taught that the original force of nature was identical with the matter out of which the universe was made.<sup>2</sup>

The history of Greek philosophy begins with Thales (c. 624-565 B.C.), a wealthy merchant. Thales and his immediate successors were not primarily evolutionists, they dealt first and foremost with the laws and origin of the universe, and also with various mathematical problems. We owe our knowledge of Thales' cosmology to Aristotle's comments. According to these, Thales taught that water was the original substance out of which everything came,

<sup>1</sup> 1942.

<sup>2</sup> *Catholic Enycl.*, 1909, Vol. 8, p. 93.

and the earth was then conceived as floating on the water.<sup>1</sup> Aristotle remarks that the same account would have to be given of the water itself which must have some kind of support. From Thales onwards the consideration of the natural laws became more and more prominent in the writings of the ancient thinkers.

Anaximander (611-547 B.C.) was undoubtedly younger than Thales; possibly he was his pupil. He directed current views of the universe into a significant and fruitful, if speculative, stage, for by his conception of the *boundless*, or infinite (Gr. *apeiron*), he created the notion of a limitless space. Out of this infinite all things came and to it ultimately returned. First there came heat and cold, next water, then air, earth and fire in this order. The earth was at its first emergence a kind of mud, living things arose from this primitive mud in a definite order—plants, animals and finally man. Moreover, man also came from another animal because infants require a much longer period of nursing than animals. According to Burnet<sup>2</sup> this animal which produced man was a fish, and the first humans appeared in the inside of it, being reared like sharks. After they had developed sufficiently they were cast out on to land. Osborn finds a germ of the evolution idea here. It certainly shows that Anaximander realised that man was not the first creature produced. Burnet considers that these views show that he had some notion of adaptation to the environment and of natural selection. According to Nordenskiöld<sup>3</sup> Anaximander is one of the pioneers of human thought because he was the first to give a natural explanation of things; grotesque as his accounts often are, they are scientific and attempt to break away from the tradition of the old mythology.

Anaximander's "boundless" was indescribable, but his successor Anaximenes (588-524 B.C.) identifies it with air which also permeated all things: it was infinite and indivisible. Normally it is invisible but changes of temperature render it visible by condensation or make it still more rarefied, as the case may be. These two ideas of condensation and rarefaction represent a great advance in ideas. Anaximenes identified the boundless with the life-force: "Just as our soul, being air, sustains us, so breath and air pervade the whole world".<sup>4</sup> Newman<sup>5</sup> tells us that Anaximenes introduced

<sup>1</sup> Aristotle, *De Caelo*, 294a, 28.

<sup>2</sup> 1930, p. 71.

<sup>3</sup> 1929, p. 12.

<sup>4</sup> Burnet, 1930, p. 73, from *Aet.* i, 34 (R.P. 24).

<sup>5</sup> 1935, p. 12.

the idea of spontaneous generation in that he taught that living things, including man, developed from the primitive slime or mud. This was also the opinion of his predecessor, Anaximander, and possibly there has been some confusion here. Diogenes of Apollonia, whose dates are uncertain, does not, strictly speaking, belong to this early school, for he was contemporaneous with later writers like Empedocles, but he held views almost identical with those of Anaximander except that air was the primary substance. He also conceived living things as emerging from the slime of the earth under the action of the sun's rays. Diogenes' own summing up of his view runs thus:—"My view is . . . that all things are differentiations of the same thing, and are the same thing".<sup>1</sup> This also sums up the fundamental feature of the whole cosmogenic and evolutionary teaching of this early Ionian school. How things came from the primordial water, air or the "boundless" they did not know, and they did not attempt to explain it further. From the point of view of evolution it seems that they recognised that living things did develop by some process of change from one order of being to another. They attempted to find the connections between the order of natural events and the origin, development and death of things, but they remained dynamists.

#### (b) *The Later Ionians*

The chief philosophers of this school from our point of view are Heraclitus, Empedocles, Democritus and Anaxagoras; they are sometimes called the physicists. The city of Miletos was sacked in 494 B.C. soon after the death of Anaximenes, so the members of this later school did not live in that town; but they upheld the traditions of the early teachers, at least to some extent. They are noted for the distinction which they made between a force moulding the world and the matter of which it was composed. Here we have a doctrine that force and matter are distinct from the very beginning, and possibly this represents the very beginnings of the ideas of mechanism.

According to Heraclitus (c. 540-475 B.C.), there was a strife of opposites in the universe because the world is "at once one and many". This apparently contradictory statement made him look for new primary stuffs. Because fire always burns steadily he considered that it produced change in the world. Thus to him all things were in constant motion, or in a state of ceaseless, unending

<sup>1</sup> Burnet, 1930, p. 353.

change moving constantly in a flux. As one thing was added to nature another was taken away. Fire becomes moist by condensation, then becomes water, which becomes earth; the earth in turn becomes water again and this, fire. Man himself is made up of these three things, fire, water and earth, and he also is subject to this process of reciprocal change. Thus in Heraclitus there is little room for evolution of species because nature is a whole in a state of constant change but yet remaining ever a whole. Nevertheless, he introduced this notion of dynamic change—a basic principle of later evolutionary theories.

Parmenides held views the direct opposite of Heraclitus. To him the world was immutable and uniform; change is an illusion. He believed only in a sensible reality. Space, or an infinite, did not exist because, as Burnet<sup>1</sup> tells us, he wrote: "Empty space is nothing and nothing cannot be thought and therefore cannot exist". To Parmenides everything *is* and therefore there cannot have been a time when it did not exist. These views of Parmenides are important because they forced later thinkers to enquire into the *nature* of change. The world may ultimately be immutable but changes obviously do take place. Thus later, Empedocles was led to explain change by movement and recombination of the four primary substances. Democritus postulated an indefinite number of atoms; modern workers consider there are some ninety primary elements; while in the most recent physics the number of electrons is regarded as indefinite.

Empedocles (495-435 B.C.) has often been called the "father of the evolution idea". With Parmenides he shares the distinction of being the only other Grecian philosopher to record his views in verse. His famous works were the *Poem of Nature* and the *Purifications*. In his attempts to overcome the difficulties created by Parmenides he discovered that air is not an empty space, but a real material entity, and that water is not condensed air. Thus he was led to postulate fire, air, water and earth as his four roots, or the primary substances, out of which all things came. These exhibited the qualities hot, cold, wet and dry. Empedocles believed in Parmenides' rule that what is, *is*, and thus these four roots were eternal. However, he did not develop any relationship between the four primary qualities hot, cold, wet, dry and the four elements. This was done in detail later by Aristotle.<sup>2</sup> Here Aristotle also

<sup>1</sup> 1930, p. 181.

<sup>2</sup> *De Gen. et Cor.*, Book 2, 1-11.

disagrees with Empedocles' conceptions of love and strife as the cause of motion.

To explain change of motion Empedocles had further to assume that two forces, attraction and repulsion, or love and hate, act in unison upon these four elements. These forces predominated, the one over the other, alternatively; in this way change was brought about. The original universe consisted of a shapeless mass, composed of a mixture of the four elements. The force of repulsion then came into action and so air was first separated and next fire. This was followed in turn by earth and water.<sup>1</sup> Life next arose spontaneously out of the earth. The first living things cast out by the force of repulsion were trees which grew before the sun was properly formed. Later there followed parts of animals, such as limbs, heads, arms, eyes, etc. The force of attraction then came into play and united these odd parts of animals, and from them arose the animals themselves. This unison of parts took place at first by chance, and so wrong parts often became united. In this way Empedocles explained the occurrence of the mythical monstrosities such as bulls with human heads, or animals with double faces. Some of these were adapted to survive, and did so, but those not so adapted died. Man arose in a similar way: at first he was thrown up by fire and repulsion as shapeless masses which gradually became limbs or other parts. But these were sexless and dumb. The parts united and later became sexed; once the sexes were separated, then distinct species arose. Reproduction started and in it the embryo received part of its substances from the mother and part from the father. Now that reproduction was established there was no further need for the earth to produce either new animals or men.

We see that Empedocles in a fantastic account of the origin of living things can be said to have arrived at the germ of the idea of organic evolution and of the theory of the survival of the fittest. He is an evolutionist because he taught that life arose gradually through an unconnected series of imperfect forms which were at first ill-adapted to live and reproduce themselves. The order of appearance—plants, animals, man—agrees also with this idea of the less perfect appearing before the more perfect. His reference to natural selection is seen in his account of the monsters which failed to survive and to those less perfect "whole-natured forms". He did not, of course, perceive the theory as we do now,

<sup>1</sup> Burnet, 1936, p. 236, from *Aet.* ii, 6, 3.

but the germ of the idea of survival must have been in his mind. This point will be discussed later when we come to consider Aristotle's contribution to evolution and biology. Nordenskiöld<sup>1</sup> says "Empedocles comes forward with a kind of doctrine of affinity, crude and clumsy it is true, but nevertheless containing within it the germ of a number of ideas which it was only possible for later ages to think out".

Democritus (c. 470-400 B.C.) was an able biologist and probably performed actual dissections. He was the founder of atomism by his conception that matter is composed of solid material particles; this was an advance on Empedocles. His chief biological studies were concerned with man, although he was probably the first to distinguish between animals with blood and those without it. While one can scarcely call him an evolutionist, he believed in abiogenesis, or the spontaneous generation of living things from the slime of the earth; he also had some idea of the meaning of adaptation of whole organs to set purposes. For example, the liver was the organ of sensuality, the brain that of thought, while the heart controlled courage.

Anaxagoras (488-429 B.C.) a contemporary of Democritus in the time of Socrates, conceived matter as originating from an infinite number of "seeds". Living things also sprang from atmospheric germs and not from terrestrial earth. He is thus the first to bring forward this view, but his general biological knowledge seems to have been scanty.

With Democritus and Anaxagoras an era in Greek science and philosophy closes. Along with Hippocrates, the founder of medicine, they also built up the beginnings of biology and, as we have seen, they grasped several fundamental principles which later became the basis of evolutionary theory. The outstanding figures among them are Anaximander, Empedocles and Democritus. They search for a natural explanation of natural happenings, and in this respect Democritus was the extremist. His doctrine seems ultimately to lead to materialism. The views of these philosophers were as numerous as themselves; there was little agreement, and no common formula. Thus they were unable to build up a unified philosophical system. Each in his own opinion was the only one who taught correct knowledge, all others held incorrect opinions. Hence, arose the Sophists. For, says Nordenskiöld,<sup>2</sup> "The claim

<sup>1</sup> 1929, p. 18.

<sup>2</sup> 1929, p. 30.



of the Sophists as to man's being the measure of all things thus for the time did away with all objective explanations of natural phenomena, for what was the use of disputing about matters which all viewed from different standpoints if all could be equally right?"

After the time of Anaxagoras no outstanding figure is encountered in biology for some time until the arrival of the giant of the ancient world, that is Aristotle.

## 5. ARISTOTLE

### (a) *General Account*

Aristotle (384-322 B.C.) was born in Stagira in 384 B.C., a Greek colony in Macedonia, where his father was court physician. Prof. J. L. Stocks<sup>1</sup> says of him: "No man or thinker is indispensable; and it is Aristotle's special glory that every thinker is his pupil, even when he does not know it". Both in the quality and quantity of his work he towers above his predecessors in most branches of knowledge, especially biology. It can safely be said of him that he founded the science of biology, or natural history, by the detailed account of animals which he gave in his famous books.<sup>2</sup> Aristotle is often described by some writers as holding evolutionary opinions, while others deny this. Because of this and because of the unique place he held among the Greek biologists, and also because of his far-reaching subsequent influence, it is necessary to treat of his work in some detail. Furthermore, a survey of his biological writings is worthwhile for the sake of their general educational value. Our primary object is to discern among his writings any tendency towards what could be described as an evolutionary viewpoint.

Aristotle's opinions in biology were based to a large extent on the personal observation of animals by himself and probably his immediate pupils. Altogether he mentioned and described well over 500 different species, excluding many lower marine animals. His observations, generally speaking, were extraordinarily acute and accurate, and he owed his success to this faculty coupled with a

<sup>1</sup> *Aristotelianism*, p. 155.

<sup>2</sup> These are as follows, the abbreviations used in footnotes are given in brackets:—*Historia Animalium* (H.A.); *De Generatione Animalium* (*De Gen. An.*); *De Generatione et Corruptione* (*De Gen. et Cor.*); *De Partibus Animalium* (*De Part. An.*). His conceptions of nature as a whole are to be found in his *Physica*, *De Caelo*, and other works; the philosophy underlying his biological theories is to be found in his *De Anima* (*De An.*).

keen, penetrating, analytical and logical intellect. His metaphysical notions of matter and form, which he applied directly to living things, were such a distinct advance on the views of his predecessors, and so obviously contained a great deal of truth in them, that he was able to evolve a unified system of thought which still stands today in many respects. In fact his great contribution to science, taken in its widest meaning, is his thought system, which includes all the phenomena of life, physical and mental. Certain it is that the foundations of his biology were solid and substantial, for they formed the basis of all biological theory, through the scholastic period up to the eighteenth century. As an example of his influence on people, even in the sixteenth century, may be quoted Sir Bertram Windle's tale of Cæsar Cremonini.<sup>1</sup> This person refused "to look through Galileo's telescope for fear of finding that Aristotle's physics were wrong".

So far in this historical account of the beginnings of evolutionary ideas we have dealt with the cosmological teachings of the various expounders. In many respects this was essential in order to grasp the meaning of the little purely biological matter with which they treated. With Aristotle, however, it was more than ever necessary to do this, because, although he has left us a biological system complete in itself, his philosophical conception of the nature of things pervades his whole system, and it is unique. A knowledge of his theory of matter and form and the relationship between them certainly helps to an understanding of Aristotle's biological ideas. And so an account of his philosophical theory is given in the appendix while in the text only the essentials are pointed out. Aristotle's concept of matter applies equally to either animate or inanimate things. By life, Aristotle means bodies having "self nutrition and growth (with its correlative decay)".<sup>2</sup> In his concept of matter he considers that what we ordinarily call substance is a composite thing made up of *materia prima* and *form*. The form of a thing transforms it from a potential state to an actual state so that it becomes recognisable by our senses. Hence living things are composite and so, as the body is the subject matter of the living thing, it cannot be the soul. Further, "the soul is the first grade of actuality of a natural body having life potentially in it. The body so described is a body organised."<sup>3</sup> Thus there are various

<sup>1</sup> Windle, 1928, p. 28.

<sup>2</sup> *De An.*, 412a, 14.

<sup>3</sup> *De An.*, 412a, 28.

grades of forms, chiefly (a) the substantial form and (b) the accidental form. The former constitutes the essence of a body, such as the catness of a cat. The latter gives the attributes to the body, such as the colour to the cat. Both forms must contribute before a thing becomes what it is.

Substantial forms themselves obviously admit of further subdivision into (a) mineral forms, giving shape to inanimate things; (b) the vegetative (plant) form, which gives the lowest attributes of life to living things, i.e., powers of nutrition and reproduction; (c) the sensitive form, which makes them capable of responding to touch, sensation, etc.; (d) the rational (or intellectual) form, which is confined to man, who also possesses each of the other types of forms whereby he (a) is, (b) is living, and (c) is sensitive. To Aristotle these forms cannot exist independent of matter.<sup>1</sup>

Whether or not Aristotle held to any idea of evolution is a controversial issue. For our purpose it is sufficient at present to notice that this theory of forms—accidental and substantial, subdivided into mineral, vegetative, sensitive, rational, pure form—gives us a series which obviously provides a basis for a rational arrangement of classifying things into mineral (inanimate), plant, animal, human and, finally, pure form. This is an ascending series with man as the earthly end point (for he possesses mind). We shall see later that Aristotle also draws up an elementary arrangement of living things on an ascending scale ending again with man. If, then, this represents an evolution of living things, so also must his arrangement of the forms represent an evolution of them. Evolution implies a change from one thing into another; but forms are not visualised as doing this, or even as being capable of it.

We can note, however, that just as an evolving species includes in itself the species from which it is evolving, so the higher Aristotelian forms include each of the lower forms attached to the same fundamental substratum of formless matter. In other words, a higher form dominates a lower one, placing the substance in a higher hierarchy of being. In the *Physica* Aristotle says:

<sup>1</sup> The scholastic, or Thomist, view is basically similar to this in that so far as the intellectual soul (or form) is concerned it can exist independently of the body, for, as the scholastics put it, "it is not wholly immersed in matter". Further, it is considered to be a doctrine of the Catholic Church that each human soul (or rational soul) is individually created and is immortal. In the higher psychic realms of the human being another form may exist, one which gives Mind, and this of all forms can exist alone, according to Aristotle. The mind is then the form of forms (see *De Anima*, 432a, 28). Compare this with the scholastic higher forms, which are the angels.

"This then is one account of 'Nature', namely that it is the immediate material substratum of things which have in themselves a principle of motion or change".<sup>1</sup> There seems to be little here to provide a basis for an argument in favour of Aristotelian Evolution.

(b) *Biology of Aristotle*

In the *Historia Animalium* Aristotle deals in detail with the parts and nature of the parts of animals. At the very beginning he opens up his subject in a thoroughly scientific manner by recognising that animals have parts which are not of equal value for descriptive purposes. The first paragraph reads<sup>2</sup>: "Of the parts of animals some are simple; to wit, all such as divide into parts uniform with themselves, as, for instance, the hand does not divide into hands, nor the face into faces". The *De Partibus Animalium* deals with the causes that determine the make up of an animal, and in book 2 Aristotle again begins by discussing the parts of animals. Here he distinguishes three "degrees of composition"—(a) formation from earth, air, fire and water, (b) homogeneous parts such as bone and flesh, and (c) heterogeneous parts such as face and hands.<sup>3</sup> Thus the parts admit of classification, and it is the possession of parts which vary in shape, nature and function which enabled Aristotle at once to recognise that animals could be classified. In none of his extant works is an actual classification given, but there seems to be little doubt from a study of his works that during his researches he realised that animals could be arranged in a series. He is always comparing groups of animals, some groups he finds are large, others small. He distinguishes between individuals, between the species, and the genus. Genera of animals are distinct but may have parts in common. "Now it is plain that if we deal with each species independently of the rest, we shall frequently be obliged to repeat the same statements over and over again. . . . A discussion, therefore, of the attributes of each such species separately would necessarily involve frequent repetitions as to characters, themselves identical but recurring in animals specifically distinct."<sup>4</sup> Aristotle spends a long time in book 1 of the *Historia Animalium* in discussing couplings of characters. In

<sup>1</sup> *Physica*, 193a, 28.

<sup>2</sup> *H. A.*, 486a, 5.

<sup>3</sup> *De Part. An.*, 646a, 12-24.

<sup>4</sup> *De Part. An.*, 639a, 20.

all of this book he seems to be analysing all possibilities of combinations, probing, as it were, for some common ground, some basic principle, on which to build up a natural, common-sense system of pigeon-holing all the various animals. In other words he is striving to find a natural classification. For example, some animals such as man and horse have blood, and all with blood either lack feet, or have either two or four of them. Other animals have no blood, examples being the bee, the wasp, the cuttle-fish, etc., and all these have more than four feet.<sup>1</sup> Again, some animals fly, and of these those like the eagle and hawk have feathered wings, others, like the bee, have membranous wings, others again, like the bat, have leathern wings.

Sanguineous flying animals have feathered or leathern wings, while non-sanguineous flying animals (bees, etc.) have membranous ones.<sup>2</sup> He suggests new genera. To Aristotle a genus was what we would call a class, i.e., a large division of the animal kingdom. He defines it as follows: "By 'genus' I mean, for instance, a Bird or Fish, for each of these is subject to difference in respect of its genus, and there are many species of birds and fishes".<sup>3</sup> Thus he notes that while all feathered forms are classed in the genus "birds", those that have membranous wings and leathern wings have no title or generic name.<sup>4</sup> Many of the characters that he used to form his groups are still used today to separate distinct groups. For example, among insects he notes (a) those which are winged; (b) those which are wingless;<sup>5</sup> and (c) those which are both winged and wingless, like the ant or glow-worm.<sup>6</sup>

The winged insects can be further subdivided into (a) those with sheath wings, the *Coleoptera*, and (b) those with sheathless wings, which themselves are further divided up into (1) those with two wings (the *Diptera*) and (2) those with four wings.<sup>7</sup> The modern classification follows this arrangement closely and recognises all of Aristotle's distinctions as of generic importance.

Emphasis is laid on the fact that all groups of animals have characters in common; even water animals and winged animals, normally two completely distinct genera, possess common features.

<sup>1</sup> *H. A.*, 489a, 30.

<sup>2</sup> *H. A.*, 490a, 6, paraphrased.

<sup>3</sup> *Ibid.*, 486a, 23.

<sup>4</sup> *Ibid.*, 490a, 12.

<sup>5</sup> *H. A.*, 523b, 18.

<sup>6</sup> *Ibid.*, 523b, 20, and *De Part. An.*, 643b, 2.

<sup>7</sup> *De Part. An.*, 490a, 14.

In dealing with cases like these Aristotle notes that groups with homologous organs are put into a single class while those with analogous ones are separated into distinct groups. "For instance, bird differs from bird by gradation, or by excess and defect, but all are feathered. Birds and fish are more remote and only agree in having analogous organs; for what in the bird is feather, in the fish is scale."<sup>1</sup> Analogies like this are universal. This is a distinction of great importance and one sometimes forgotten in modern evolutionary writings. Contrast this view of Aristotle's with, for example, that of Pycraft<sup>2</sup> who attempts to derive the avian feather from the reptilian scale, i.e., he makes these dermal appendages genetically related.

Thus Aristotle's genera comprise these large classes like birds and fishes, each of which is made up of an assemblage of individual types, the species. These species are the real existences and form recognisable units. Those within a genus differ only in degree in respect of contrasted conditions like rough, smooth, or small and large, etc.<sup>3</sup> Aristotle disagreed with the dichotomous methods of classifying things, because, as he says, "It is impossible to reach any of the ultimate original forms by dichotomous division".<sup>4</sup> He discards such methods because each single ultimate branch ends in a single character (or *differentia*), and no species possesses only one character as a distinguishing feature. Throughout his books, and especially in his introductory parts in the *De Partibus Animalium*, book 1, sects. 2, 3 and 4, he seems to be looking for a basis on which to build up a *natural* classification, showing the true relationship, if any, between species, as opposed to an artificial system of dichotomy. For a guide in this endeavour he relies on the natural instinct of men to form the larger obvious groups (genera). "The method then that we must adopt is to attempt to recognise the natural groups, following the indications afforded by the instincts of mankind, which led them, for instance, to form the class of birds, and the class of fishes, each of which group combines a multitude of *differentiae* and is not defined by a single one as in dichotomy."<sup>5</sup> It must be emphasised that Aristotle nowhere gives such a thing as a table of classification. Any such tables purporting to show his schemes are merely compilations from scattered parts of various texts. The compiler is expressing

<sup>1</sup> *De Part. An.*, 644a, 20.

<sup>2</sup> 1899, p. 236.

<sup>3</sup> *H. A.*, Book 1, 1, and *De Part. An.*, Book 2, 1-4.

<sup>4</sup> *De Part. An.*, 644a, 10.

<sup>5</sup> *De Part. An.*, 643b, 10.

what *he* (with his more modern knowledge) thinks were the ideas of Aristotle in this respect which were guiding him during his work in Biology. It is rarely that we find such a sentence as the following in Aristotle: "Here we must make our first start from the first class; these are the perfect or viviparous animals, and of these the first is man."<sup>1</sup> His primary divisions are plants, animals and man. Plants can grow and reproduce, and thus possess life; indeed, their purpose in life is to form seed and fruit. They get their food from the earth, it is elaborated for them, and thus they do not produce any excrement—the earth and its heat serve as their stomach.<sup>2</sup> They arise either by spontaneous generation from the earth, or from some other plant, or from seed.<sup>3</sup> Sexes in plants, however, were not distinctly recognised. Their form is vegetative. Animals also grow and reproduce and thus possess a vegetative form, but they are also sensitive, and hence possess a sensitive form. Man, of course, stands apart because of his possession of intellect and mind, but he is still part of the animal kingdom; he is in fact an isolated species.

A detailed account of Aristotle's classificatory treatment of animals is given in the appendix. His notions of the positions of animals in the organic world are obviously founded upon his preconceived philosophical ideas. In his biology this means that he perceives a scale of perfection of being among animals. The extracted classification given in the appendix which is based chiefly on the reproductive features, and among the lower forms on other somatic characters and habits, gives us a graded series of animals beginning with those which Aristotle himself considered intermediate between plants and animals, the zoophytes, which reproduce only by means of spontaneous generation, scolex, imperfect eggs, ovipary with imperfect eggs, ovipary with vivipary, ovipary with perfect eggs, and true vivipary ending in the most perfect of creatures—man. The position of those creatures, the insects, reproducing by means of the scolex is interesting because they come immediately next to those which are either plant-like or come from the earth by means of spontaneous generation. Aristotle probably regarded the scolex as the ultimate means whereby all animals are produced, even man. It is fitting then that the insects should be placed next to those animals which come straight from the slime of the earth.

<sup>1</sup> *De Gen. An.*, 737b, 26.

<sup>2</sup> *De Part. An.*, 650a, 20.

<sup>3</sup> *De Gen. An.*, 715b, 27.

(c) *Aristotle and Evolution*

We are now in a position to judge whether or not Aristotle was an evolutionist. The answer to this problem is important, because the teachings of this great teacher stood unchallenged for many centuries, especially his biological findings. They were accepted without question. Hence, if we find that Aristotle is not an evolutionist, then we have at least a strong clue as to the real reason why the subject of theoretical biology did not develop as quickly as many of our moderns would have liked it to.

It is frequently asserted in textbooks of biology that Aristotle was a believer in evolution, and furthermore that he taught a system of evolution. Possibly this view became popular because of H. F. Osborn's statement in his book *From the Greeks to Darwin*.<sup>1</sup> Some other writers who support this view are Nordenskiöld<sup>2</sup> and H. H. Newman,<sup>3</sup> while Charles Singer<sup>4</sup> leans in that direction. For instance, Nordenskiöld,<sup>5</sup> referring to the works of Aristotle, says: "here we find enunciated for the first time a really complete theory of evolution", while Osborn<sup>6</sup> is no less dogmatic when he states: "These passages seem to contain absolute evidence that Aristotle had substantially the modern conception of the evolution of life from a primordial soft mass of living matter to the most perfect forms, and that even in these he believed evolution was incomplete for they were progressing to higher forms." Recently the question has been reviewed by Torrey and Felin,<sup>7</sup> who dispute these views and cite others to support their own view such as T. E. Lowes,<sup>8</sup> A. W. Benn,<sup>9</sup> and A. E. Taylor.<sup>10</sup> Let us examine the evidence.

Empedocles in the *Poem of Nature* is quoted by Aristotle<sup>11</sup> as saying "wherever then all the parts came about just what they would have been if they had come to be for an end, such things survived, being organised spontaneously in a fitting way; whereas

<sup>1</sup> 1924.<sup>2</sup> 1929.<sup>3</sup> 1935.<sup>4</sup> 1931.<sup>5</sup> 1929, p. 37.<sup>6</sup> 1924, p. 57.<sup>7</sup> 1937.<sup>8</sup> 1912.<sup>9</sup> 1914.<sup>10</sup> 1925.<sup>11</sup> *Physica*, 198b, 28 to 33.



those which grew otherwise perished and continue to perish, as Empedocles says his 'man-faced ox-progeny did'."

This passage seems to hint at natural selection, as we will see below. Aristotle was well acquainted with such freaks, but later on in the same book of the *Physica*, rather than admit natural selection, he states that Empedocles' monstrosities failed to survive because of some corruption in the seed (i.e., semen or germ cells), for the seed must have existed previous to the animals.

In the *De Partibus Animalium*<sup>1</sup> Aristotle further emphasised this when referring to Empedocles' mechanical explanation of why the backbone is divided into vertebræ by pointing out that a creative seed containing certain developmental potentialities is necessary for propagation. This corruption in the seed which Aristotle refers to seems to be a close approximation to our modern ideas on the occurrence and effect of lethal factors which, under certain circumstances, bring about the very early death of the embryonic organism, but it is scarcely due to the effect of natural selection. The passage in the Oxford translation<sup>2</sup> by R. P. Hardie and R. K. Gaye reads: "Further, seed must have come into being first, and not straightway the animals; the words 'whole-natured first' . . . must have meant seed". Osborn considers this one of the passages purporting to show that Aristotle was an evolutionist. He used Taylor's<sup>3</sup> translation which reads as follows:—"Further still it is necessary (i.e., according to law) that germs should have been first produced and not immediately animals and that soft mass which first subsisted was the germ".<sup>4</sup> Osborn apparently takes this "soft mass" to be the primitive and undifferentiated stuff out of which all things were made. Several commentators, as Torrey and Felin<sup>5</sup> point out, have shown that these words refer to Empedocles' views; they were not Aristotle's—the latter was actually quoting them. The translation of Hardie and Gaye mentioned before renders Taylor's "soft mass" by "whole-natured first", and they give the reference to Empedocles as Fragment 62. 4. While Burnet<sup>6</sup> after Diel<sup>7</sup> translates them as "whole-natured forms first". He also gives the reference to

<sup>1</sup> 640a, 23.

<sup>2</sup> *Physica*, 199b, 7.

<sup>3</sup> *The Works of Aristotle*, 6 vols.

<sup>4</sup> Osborn, 1924, p. 56.

<sup>5</sup> 1937.

<sup>6</sup> 1930, pp. 214 and 243.

<sup>7</sup> 1879.

Fragment 62 of Empedocles' works. Empedocles at this point in his poem is discussing the evolution, or rather the *development*, of animals and has reached the third of the four stages. Incidentally, these whole-natured forms are composed of water and earth. Furthermore Aristotle believed in spontaneous generation, and he considered that it occurred at all times and not just from a primordial mass.

As Burnet points out,<sup>1</sup> the passage quoted above<sup>2</sup> seems to hint at natural selection, or the survival of the fittest. Here Aristotle is discussing the necessity for purpose in nature, and he rejects this idea of Empedocles as an argument which, if accepted, seems to show that adaptations are produced by chance. Nature, he concludes, does act for an end, is purposive. But Empedocles' bulls with human heads could be lethals and thus unable to survive from the very beginning. Aristotle here expresses what W. R. Thompson<sup>3</sup> calls a truism, namely, that adaptations *qua* adaptations couldn't survive unless they were adapted to live. If Aristotle had continued to develop this argument he might conceivably have been led to the view that, of a number of small differences, all adapted by nature, some may have been better adapted, and hence selected by nature, than others, which does not necessarily exclude purpose in nature, or prevent the appearance of monstrosities. According to Osborn<sup>4</sup> if Aristotle had accepted Empedocles' views "he would have been the literal prophet of Darwinism".

Aristotle, however, did not pursue this topic on these lines; instead he continues in an argument designed to show that nature does not work by chance, but always works for an end. This purpose in nature is seen in plants as well as in animals, though the degree of organisation is less in the former. Nature is a cause operating for a purpose. "But when an event takes place always, or for the most part, it is not incidental or by chance. In natural products the sequence is invariable, if there is no impediment. . . . It is absurd to suppose that purpose is not present because we do not observe the agent deliberating. Art does not deliberate. . . . If, therefore, purpose is present in Art, it is present also in nature. The best illustration is a doctor doctoring himself".<sup>5</sup>

There are a few other places where Aristotle shows that he appreciated the pruning effects of nature on organisms which produced large numbers of eggs. Indeed, an egg, like that of a

<sup>1</sup> 1930, p. 242.

<sup>2</sup> *Physica*, 198b, 28.

<sup>3</sup> 1937, p. 192.

<sup>4</sup> 1924, p. 57.

<sup>5</sup> *Physica*, 199b, 24-30.

fish, is imperfect because, due to the large number of eggs formed and the small size of the uterus, they are shed before they have had time to develop.<sup>1</sup> The uterus is too small to hold them. Aristotle remarks<sup>2</sup> that if all the eggs laid developed, each species would be infinite in number. This is obviously an appreciation of the fact of over-production among nature's reproductive cells. Most of the fishes' eggs do not develop because the male eats some of them, some waste in the water; only those fertilised by male sperm develop, "while the rest are left to their fate".<sup>3</sup> While Aristotle thus had knowledge of over-production among species he did not develop it into an idea of natural selection, which surely seems to be the next logical step. In the theory of natural selection it is the young organism that is mostly visualised as being selected. True, nowadays the theory has been extended to include even the germ plasm. We are left to assume that it is a matter of chance which group of eggs receives the sperms shed by the male fish. There is no hint, however, that any of the eggs possess combining advantages over any of the others, or are better adapted than others for resistance to death by natural means. In another place<sup>4</sup> Aristotle tells us that the fishes' eggs, after being cast out from the fish, grow quickly because of the danger of perishing. "Hence the class of fishes is prolific, for nature makes up for the destruction by numbers."

The actual passages in Aristotle which seem to give the proof that he was an evolutionist are the following :—1. "Nature proceeds little by little from things lifeless to animal life in such a way that it is impossible to determine the exact line of demarcation, nor on which side thereof an intermediate form should lie".<sup>5</sup> 2. "For nature passes from lifeless objects to animals in such unbroken sequence, interposing between them beings which live and yet are not animals, that scarcely any difference seems to exist between two neighbouring groups owing to their close proximity."<sup>6</sup>

If a modern writer were to write these passages no one would doubt but that he was expressing a belief in evolution. Does it necessarily follow that Aristotle was doing likewise, or even that he meant that these passages should be taken as indicating some kind of descent with modification? Let us see.

<sup>1</sup> *De Gen. An.*, 755a, 22.

<sup>2</sup> *H.A.*, 567a, 31.

<sup>3</sup> *Ibid.*, 567b, 6.

<sup>4</sup> *De Gen. An.*, 755a, 31.

<sup>5</sup> *H.A.*, 588b, 4.

<sup>6</sup> *De Part. An.*, 681a, 12.

When we realise that Aristotle's biological ideas were founded on his metaphysical concepts of matter and form we have the clue to the meaning of the above passage. There is a hierarchy of forms starting with the form giving being to lifeless matter, and so on through the forms of plants, animals to man. Nature does produce things in a sequence of *perfection* according to the types of form infused into the matter whereby it gets its actuality. But its perfection depends also on the actual components of the primary elements, qualities and contrarieties which go to make up its body. For instance, the serpents and birds are hot and produce a perfect egg, but they are also dry. If they had been hot and wet they would have been viviparous, a more perfect type. It is the form which is the dominating agent because it is the final cause of the body;<sup>1</sup> it gives the power of locomotion if present, and sensation, and the powers of nutrition and reproduction.<sup>2</sup> The form, however, is immutable, especially the human soul, because, intellectually, it seeks after a knowledge of the abstract, and hence transcends matter. In a sense then we should say that there is an evolution of forms—lifeless, plant, animal, man. Thus we must find out how it is that they can be arranged in this serial manner which certainly agrees with the order in which an evolutionist would place them.

This serial arrangement is the natural one because of the attributes which each form gives to the material body. In the case of lifeless matter the form gives it mere actuality; in the case of plants the requisite form gives the power of nutrition and reproduction, for, as Aristotle<sup>3</sup> says: "the nutritive soul then must be possessed by everything that is alive". Thus a plant possesses the form which makes it actual and which makes it a vegetable. In the case of animals the form making it such gives the attributes of sensation. "But animals must be endowed with sensation, since nature does nothing in vain", it must be able to feel if it is to survive.<sup>4</sup> Animals are also actual and able to feel if they are to survive.

<sup>1</sup> *De An.*, 415b, 15.

<sup>2</sup> *De An.*, 415b, 23 and 416a, 18.

<sup>3</sup> *De An.*, 434a, 22.

<sup>4</sup> *De An.*, 434a, 30; the full passage reads: "But animals must be endowed with sensation since Nature does nothing in vain. For all things that exist by Nature are means to an end, or will be concomitants of means to an end. Every body, capable of forward movement would, if unendowed with sensation, perish and fail to reach its end, which is the aim of Nature: for how could it obtain nutriment?" A similar passage is found in the *De Anima*, 434b, 12, as follows: "An animal is a body with soul in it; every body is tangible, i.e. perceptible by touch; hence necessarily if an animal is to survive, its body must have factual sensation."

Animals are also actual and nutritive and hence possess these forms also. We note here that those organisms like sponges which are intermediate between plants and animals (according to Aristotle) possess some kind of sensation. In fact Aristotle finds in the animal world a graduated differentiation in sensibility<sup>1</sup>. Finally, in a like manner, man possesses these forms plus that which makes him rational, a thinking being.

There is no question here that nutritive form is descended from the vegetative, or the intellectual one from the nutritive. Such a conception would be anathema to Aristotle. If then we wish to find evidence of Aristotle's evolutionary leanings we must proceed along a different path, for the series of forms gives us no justification for concluding that plant, animal, man represents an evolutionary genetic sequence. This conclusion finds further support when we consider that any one of these organisms, even man, could arise spontaneously from the slime of the earth, or so Aristotle thought. The mere fact that the form is unchanging is itself weighty evidence against Aristotle's supposed evolutionary views. In fact Aristotle considered the form immutable. Torrey and Felin<sup>2</sup> emphasise this fact and point out that it is of fundamental importance. They also remark that those writers, like Osborn,<sup>3</sup> Locy,<sup>4</sup> Newman,<sup>5</sup> and Nordenskiöld,<sup>6</sup> who consider Aristotle as a "racial evolutionist", ignore this most important point. Each individual plant, or animal, or man, is perishable, but as each one strives towards a common goal, that is, to partake in the eternal and divine, then the "most natural act is the production of another like itself, an animal producing an animal, a plant a plant, in order that, as far as its nature allows, it may partake in the eternal and divine".<sup>7</sup> In spite of the contents of the passages quoted on page 28, there is no question here of a plant *producing* an animal. It is only by generation that a perishable individual of a species can become eternal and immutable.<sup>8</sup> This is a similar type of argument to that used by those who consider that such unicellular organisms as the amœba, which divides continually by fission, are potentially immortal. The undeniable fact is that there is no conception of evolution here.

<sup>1</sup> *H.A.*, 588b, 17.

<sup>2</sup> 1937, p. 12.

<sup>3</sup> 1924.

<sup>4</sup> 1908.

<sup>5</sup> 1935.

<sup>6</sup> 1929.

<sup>7</sup> *De An.*, 415a, 30.

<sup>8</sup> *De Gen. An.*, 741b, 32.

How is it that Aristotle arranged, or seemed to arrange, living things in a series which resembles our modern evolutionary sequence? The only way in which Aristotle could pursue his biological studies was by observation of their characteristics. Thus he was, like Linnaeus, able to define groups merely because the members of a group possessed some characters in common. As J. R. Ainsworth Davies<sup>1</sup> remarks, a classification of this type assumes the existence of sharp boundary lines; hence it is not primarily a natural grouping.

The Aristotelian series of the kind given here is not one based on proven (or suspected) genetic relationship, but it may at least show some possible connections; while in the scale of perfection the changes encountered from the lowest point to the highest point in the series do show, in the scale of morphological characters, a series of gradations. Hence such a scheme may have some evolutionary value to more enlightened generations, but it does not commit the original author to such views. Aristotle does seem to be striving to find some basis for a concise classification of animals, but he never actually achieved this aim. He is prevented from this by his preconceived principle that species are immutable. Nevertheless, by making use of the way in which animals bring forth their young, he comes very near to its realization. It is possible that he foreshadows the doctrine of biogenesis, because he seems to recognise that embryology gives evidence as to the affinities of animals. He recognises all insects as a group reproducing by means of a scolex. The bony fishes are a separate group from the cartilaginous ones and they reproduce rather differently. *Batrachus* is here an intermediate type: Aristotle is uncertain in which group of fishes to put it, for it has affinities with both. The whales and dolphins Aristotle recognises as a separate and distinct group of the higher animals because they have viviparous reproduction (besides other features); they are not fishes but *Cetacea*. In this sense only does such a series as Aristotle's show any degree of evolutionary relationship between the various members.

Finally, this brings us to a consideration of what Aristotle means when he says that such and such a thing is intermediate between plants and animals. In modern textbooks, if the statement is made that B is intermediate between A and C, it either means that B is descended from A and C, or that the series A, B, C form a genetic series. Did Aristotle mean either of these?

<sup>1</sup> 1903, Vol. 1, p. 10.

The following groups are said to be intermediate between plants and animals—sponges, holothurians, *Acelephæ* and testaceans. The sponges Aristotle considers to be almost purely vegetative; the holothurians are slightly sensitive, otherwise they are the same as the sponges. These forms are attached to some substratum such as rock; they do not void any visible excrement. Hence they resemble plants. The *Acelephæ* are definitely sensitive but some kinds are rooted like plants, others are free-moving like animals. All reproduce by means of spontaneous generation. The *Testacea* are intermediate for they “perform the function of neither class as belonging to both. As plants they have no sexes and one does not generate in another; as animals they do not bear fruit from themselves like plants; but are formed and generated from a liquid earthly concretion”.<sup>1</sup> Some of them are free, but others like the ascidians and limpets are attached. They reproduce in several ways (which is to be expected from their intermediate position). The *Testacea* stand in the same relation to water as plants stand to earth, for few of them live on land and few plants live in the water. In other words, as Aristotle says, “plants and *Testacea* are analogues”.<sup>2</sup> It is in this sense then that Aristotle considers them (and other lowly creatures) intermediate between plants and animals. There is no hint at all that the condition of intermediacy implies any true relationship between them, i.e., the series *plants*, *Testacea*, *animals* do not form an evolutionary series. Indeed, it is only by considering that plants and *Testacea* are analogous that we can understand the methods of reproduction in the latter group. Each method of reproduction in the one group has its analogue in the other group. For instance, some *Testacea* are formed by spontaneous generation; others by budding analogous to plants producing buds, like the onion; others spring from a generative slime analogous to the seed of plants.

Summing up, it seems most probable that there is little concrete evidence that Aristotle believed there was an evolution from “polyp to man” as Osborn puts it. Certainly he may have had dim ideas about such a process but only in so far as a convenient serial classification could be produced—classification implying no actual *relationship*, however remote. The basic principle of the immutability of species prevented him from envisaging one species as being produced from, or turning into, another species. The

<sup>1</sup> *De Gen. An.*, 731b, 7.

<sup>2</sup> *De Gen. An.*, 761a, 26.

possibility of compiling a serial classification of the actual living organisms is dependent on a natural hierarchy of the important forms, and there is no possibility of these evolving. These forms give the primary attributes which make the matter actual, and a living thing what it is. All other attributes are superficial and basically unimportant; as Aristotle says,<sup>1</sup> "all other senses are necessary to animals, as we have said, not for their being, but for their well-being". On this view it is difficult to imagine that mere change in such secondary characters could be responsible for guiding the destiny of a species.

This conclusion is in harmony with the only one we can draw from the Aristotelian cosmological ideas where the universe is considered to be unchanging, but existing with a continuous material basis in which the fundamental substances are the primary elements, earth, air, fire and water. Motion is imparted to the universe by an immaterial First Cause. These four elements are also the fundamental elements in the living world, and if this latter were to be considered as evolving, then surely the universe must also be evolving. But as Torrey and Felin<sup>2</sup> assert, "It is clear that such a universe, rigid, uncreated and immutable, left no opportunity for the ceaseless differentiation of which the plastic universe of the Ionians was capable. Whatever Aristotle's understanding of the ways of terrestrial nature, it does not seem possible by the farthest stretch of imagination, to reckon him among the cosmic evolutionists."

## 6. THE POST-ARISTOTELIANS

After Aristotle, the study of biology steadily declined due, to some extent, to the activities of the conqueror Alexander, during which time Greece was overrun. From the time of Aristotle very little, if any, real advance was made in evolutionary theory up to the time of the seventeenth century.

Theophrastus (370 B.C.) has been called the father of modern botany in that he gave descriptions of many plants, but it can scarcely be said that he had any idea of evolution. As he was Aristotle's pupil, inherited his garden,<sup>3</sup> and succeeded him at the Lyceum, one would expect some sort of classification to emerge from his works, the *Historia Plantarum* and the *De Causis Plantarum*. We

<sup>1</sup> *De An.*, 435b, 20.

<sup>2</sup> 1937, p. 8.

<sup>3</sup> R. J. Harvey-Gibson, 1919.



would expect this even more if Aristotle had conceived of the idea of evolution. But Theophrastus' writings show no signs of any groupings such as we can extract from the *Historia Animalium*. The only classifications that Theophrastus gives are purely artificial ones, such as the division of plants into trees, shrubs and herbs; or into aquatic, terrestrial, marshy plants, marine plants, and so on. This fact in itself is evidence that the Master did not conceive of the idea of evolution either. The use of the flower as the basis of classification did not emerge until Valerian Cordus (1515-1544) in his *Historia Stirpium* suggested it. His suggestion, however, was ignored, as Singer<sup>1</sup> tells us, until the eighteenth century. In the botanical world no one improved on Theophrastus' classification until Cesalpino (1519-1603) wrote his *De Planta* (1583). In this book he did approach a natural classification by making use of the characters of the flowers, fruits and seeds.

Epicurus (341-270 B.C.) contributed nothing to the idea of evolution. He was a supporter of Democritus and Empedocles, and hence opposed any theistic conception of nature. Lucretius (99-55 B.C.) was a Roman, who wrote in verse, and his main contribution was a summing up of pre-Aristotelian teachings on nature. His opinions were anti-teleological and atheistic. He certainly did not foster any evolutionary ideas, for he believed that plants and animals could arise fully formed from the earth by spontaneous generation. The stoic Pliny, born in A.D. 23, produced a voluminous *Natural History*, and in it he dealt with animals; but merely the habits and characteristics of these are given in an irregular sequence. The last of the Greek Naturalists were Galen (131-200 A.D.) and Dioscorides, whose dates are uncertain. The former followed on Aristotelian lines closely, but he did not believe in the creation of anything out of nothing. Thus he was led to deny the Mosaic account of creation. The latter catalogued many plants of medicinal value. Neither of these two writers contributed anything to the conception of evolution.

The so-called Dark Age of western culture extended from about 400 A.D. to 1000 A.D., and this is included in the mediæval period extending up to about 1400 A.D. The works of Aristotle were then in process of translation into Latin from the Arabic, and so the Dark Age merges into the period of Scholasticism. The early Fathers of the Church all lived before 400 A.D., and so are not included in the Dark Age. During this period biology

<sup>1</sup> 1921, p. 8.

advanced but little, if at all; the biology of the Greeks was accepted as standard. The Early Christians and scholastics alike had little time for studies of external nature. Singer<sup>1</sup> tells us that St. Augustine was responsible in a great measure for this sudden withdrawal from the study of nature. As this great saint said: "Go not out of doors, return into thyself. In the inner man dwells truth". The learning of this period was confined to the study of theology, the combating of heresies, and in laying the foundations of the Catholic religion. Thus, just as in the early Greek period, there was no coherent philosophical system, for many divergent views were held.

The rise of Mohammedanism in the West gave an Arab culture which was seen to be chiefly experimental in nature, and more particularly interested in astronomy. The Arabs translated Aristotle into Arabic, and the chief naturalists among them are Avicenna (980 A.D.) and Averroes (1206 A.D.). Avicenna was a Persian who exerted a considerable influence on the progress of knowledge in the natural sciences. He follows the principles of Aristotle fairly closely in that he holds that there is purpose in nature. Averroes also followed Aristotle. In fact, the Arabian culture in general seems to have taken over Aristotle as the Master. It was this fact that made the Church hesitate for so long before absorbing Aristotle, because of the difficulty of disentangling true Aristotelian teachings from the Arabian corruptions, which were, of course, tinged with Mohammedanism. Nevertheless, in the mediæval universities, Latin versions of Arabic translations of Aristotle were long used.

The scholastics rationalised the views of their predecessors; St. Thomas Aquinas and Albertus Magnus ultimately based their system on Aristotle's, just as Aristotle himself had rationalised the earlier Greek science. Thus many of the views of Aristotle persisted even right up to the seventeenth century, and his biological views were never seriously questioned for hundreds of years. After passing into the hands of the Arabs his views were absorbed by the schoolmen of the Middle Ages, but not without much hesitation. Nordenskiöld<sup>2</sup> states: "Thus it came about that Aristotle, the founder of systematic biology, became at the same time the father of the Scholastic Philosophy of the Middle Ages; that the man who was the first to introduce and logically to apply to the conception of the entire universe a theory of evolution from the

<sup>1</sup> 1941, p. 124.

<sup>2</sup> 1929, p. 43.

lower to the higher appeared fifteen centuries later as the founder of a system of stagnation and obedience to authority". It is because of the rather common occurrence of such printed matter as this that it has been necessary to consider Aristotle in some detail. The idea behind such writings is obvious. Aristotle may be looked upon as the father of Scholastic philosophy. His great pupil was St. Thomas of Aquin, who was given the unique title of Angelic Doctor because of his great and outstanding contributions to Catholic philosophy and theology. St. Thomas, like the other scholastics, merely accepted the current and Aristotelian biological teachings. The scholastics were theologians and philosophers, not professional biologists. Aristotelian philosophy was absorbed in part because much of its terminology enabled the schoolmen to express the philosophy and theology of the Church in a concise and logical manner. It fell into a period of decline possibly because what was needed at the time were new ideas about the physical and natural world; but these were not forthcoming from the naturalists of those times.<sup>1</sup>

Again, referring to the sentence quoted above, we can agree with the writer that Aristotle was, in a sense, the founder of systematic biology, but we have also seen what is the value of the statement that the Greek philosopher was the founder of a theory of evolution. To Aristotle, because of his theory of matter and form, the conception of evolution could only have been illogical and meaningless.

<sup>1</sup> The source of the error in such statements as this is simply found. It lies in the confusion in the mind of the writer of those very different subjects, namely, scholastic theology and scholastic philosophy. This confusion is fairly widespread; and much of it is no doubt due to the fact that the teachers of scholastic theology were often also the teachers of scholastic philosophy. It is not, therefore, surprising that the error has spread to some scientific writers. As Windle (1928, p. 38) says: "To confound Scholastic philosophy with Scholastic theology is to confound the examination of natural truths by reason with the study of Christian dogma—as if Scholasticism were only, as Bruker expresses it, a discussion of revealed mysteries by the light of the badly understood principles of Aristotelianism." Philosophy of any kind is not subject to any authority except that of our reason, but theology, depending in the final analysis on revealed truth, is naturally enough, subject to authority. We arrive at the authenticity of revealed truth by the "unaided light of our human reason", as St. Thomas argues (*Summa Contra Gentiles*, chap. 7, paras. 1 and 7): "Now though the aforesaid truth of the Christian faith surpasses the ability of human reason, nevertheless those things which are naturally instilled in human reason cannot be opposed to this truth. For it is clear that these things which are implanted in reason by nature, are most true, so much so, that it is impossible to think them to be false. . . . From this we may evidently conclude that whatever arguments are alleged against the teachings of faith, they do not rightly proceed from the first self-evident principles instilled by nature."

## CHAPTER 2

### THE SPECULATIVE PERIOD UP TO 1790 A.D.

#### 1. THE EARLY CLASSIFIERS

THE first biologists after the mediæval period, that is, of the Renaissance, were still followers of Aristotle, or other writers, such as Pliny the Elder. The most important of the post-mediæval biologists were Edward Wotton (1492-1555), who wrote a descriptive catalogue of animals called *De Differentiis Animalium*, and Gesner (1515-1565), who produced a voluminous *Historia Animalium* of four large volumes. Gesner followed the method of Aristotle but he was the first naturalist to make use of original illustrations of some of the animals he described. Neither of these men, or any of their contemporaries, like Aldovardi, or Gerard in his *General History of Plants* (1597), could be called evolutionists. In their writings they followed Aristotle and their classifications were purely arbitrary. For instance, Gerard classified plants according to the degree of their usefulness to man.

Hence these men were essentially compilers of information, giving lists and descriptions of plants and animals. They were soon followed by the true classifiers, who attempted to make their classifications less arbitrary. The first of these was Cesalpino, who first recognised botany as a distinct subject, or branch of natural science. The word botany had not yet been invented. From this time onwards the idea of classification becomes increasingly important until it permeates the whole field of a quickly developing science. At first it is artificial. Later the concept of true relationship, or affinity, between organisms comes in; so that the tendency then is to construct a natural phylogenetic classification expressing the evolutionary history of plants or animals concerned. Modern systematists are still striving to do this at the present time.

#### 2. SEVENTEENTH AND EIGHTEENTH CENTURY CONTRIBUTIONS

In the seventeenth and eighteenth centuries there was an outburst in the study of science approached from several angles.

A large number of writers published their ideas and findings. Chronologically, both Buffon and Lamarck belong to the latter end of this period. The former, who was one of the greatest men of the times, does not fit easily into any of the three groups given below, into which most of the naturalists of the period can be placed. His writings, indeed, form the bridge between the thinkers of this speculative period and the following one. For this reason his works have been treated separately. Lamarck, on the other hand, definitely belongs to the period after 1790, and so we will consider his contributions to natural history in the next chapter.

Excluding these two men, in the biological literature of the period, three main types of writers can be picked out. These are—

- (a) *Naturalists*, like Ray, Tournefort and Linnæus;
- (b) the purely *Speculative Writers*, like de Maillet, Diderot and Oken;
- (c) the *Natural Philosophers*, like Bacon, Descartes, Leibnez and Kant.

None of these, with the possible exception of Kant, are really evolutionists, but the members of each group are of importance from our general point of view. The Naturalists, by their classifications, blazed the trail as it were for the later biologists to whom the idea of evolution was becoming more and more the great unifying principle of their subject. The Speculative Writers were wild in their speculations, often using Greek ideas as the basis of their arguments. In many ways they correspond to some of our present day writers who popularise science and treat of theories and suggestions as if they were concrete well established facts. We will consider them quickly. Finally we will treat of the Natural Philosophers who, as philosophers, have sometimes been called the prophets of science in that they undoubtedly helped to lay the foundation stones of the modern evolution idea by their insistence on natural causation for natural events. The advent of these philosophers marks the definite break with scholasticism, which, by now, was without doubt waiting for the emergence of new scientific ideas.

#### (a) *The Naturalists*

Cesalpino (1519-1603) used an entirely new method of classifying plants. He was a physician, philosopher and botanist who was well versed in Aristotle and his commentators. In 1583 he published his *De Plantis Libri*. In it he described many original observations

which he had made on plants, especially on their flowers, fruits and seeds and the form of the flowering shoot. These characters are compared from plant to plant. Together with the characters of the cotyledons and the embryo they formed the basis of his classification. Unfortunately, like his predecessor Gesner, he still retained the convenient division of plants into trees, shrubs and herbs. According to Linnæus he was the first to lay down a real basis for classification.

Cesalpino's system was based on the type of a single or of a few organs. Thus it is artificial. He was followed by Baudin (1550-1624). Of him, Nordenskiöld<sup>1</sup> tells us that he was the originator of a natural plant classification because he grouped plants according to their likenesses as a whole to each other. Thus he was able to recognise such natural groups as the *Gramineæ*, the *Liliaceæ* and the *Zingiberaceæ*. Rivinus invented an artificial system based on the characters of the corolla.

Meanwhile in England, John Ray (1627-1705) was occupied with his researches which led to several publications, culminating in the great work the *Historia Plantarum*, published between 1686 and 1704. Ray still clung to the old divisions of trees and shrubs. The latter are subdivided into flowering and flowerless plants, while the former comprised the dicotyledons and the monocotyledons. Trees were also put into similar groups. From all these groups he formed thirty-three classes, some of which were natural ones. Ray recognises genera and he knew that the monocotyledons had parallel veins in their leaves.

Ray was followed by Tournefort (1656-1708), who improved his botanical classification by emphasising the importance of genera. Like Ray, he continued to base his system on the characters of the flowers and fruits. He found that the varying characters of root, stem and leaf were only of use for delimiting species, but he still retained the old primary divisions of trees, shrubs and herbs. The chief part of the flower which he used in classification was the corolla. Here he recognised that it could be gamopetalous, or with fused parts, polypetalous, or with free parts, cruciform, or in the form of a cross, etc. Thus his system was artificial.

The last great plant classifier of the speculative period of evolution was Linnæus (1707-1778), whom we will now consider. The work of this outstanding man is well known; his really great contribution to biology was the system of binomial nomenclature which he introduced. Previous to Linnæus, Tournefort had given

<sup>1</sup> 1929, p. 194.

each genus a name, but the species in the genera were still described by a summary of their individual characteristics. Obviously this method was very cumbersome.

During these centuries the world was being explored widely; thus inevitably new species of plants and animals were being continuously found. Hence the old method of describing them proved to be too long and difficult to remember. Attempts were made to overcome this difficulty by making drawings of the plants. This was the time when many botanists were famous collectors of plants. For example, Dr. John Fothergill (1712-1780) built his own botanical gardens.<sup>1</sup> Sir Joseph Banks (1743-1820), a past president of the Royal Society, considered that this garden was only equalled anywhere by the Royal Botanical Garden at Kew. Fothergill stocked his garden with all the rare plants that money could buy, and he employed several artists to make drawings of them, especially the new species.<sup>2</sup> Linnæus overcame this difficulty of describing organisms by enumerating the organs of each species in a regular and consistent manner in his *Philosophia Botanica* (1751). In 1753, in his *Species Plantarum*, he gave each species a name which was coupled to the name of the genus to which it belonged. Thus the dog rose was the species *canina* of the genus *Rosa*; hence its botanical name was given as *Rosa canina*. Without this advance it would have been impossible to evolve a truly satisfactory classification in future years, for the number of species was continually increasing. Linnæus thus gave status to the species and to the genus; while the very fact that he recognised that there were genera with contained species implies that he realised that there was some sort of affinity between them.

In 1735 he published his *Systema Natura*, in which he classified plants according to their sexual system. This was an artificial classification depending simply on the number, characters and arrangements of the stamens in the various flowers. Linnæus was led to believe that the stamens were important characters in plant classification after the experimental discovery of sexuality in plants by Camerarius (1665-1721) in 1694.<sup>3</sup>

<sup>1</sup> See R. Hingston Fox, *Dr. John Fothergill and His Friends*, 1919.

<sup>2</sup> Incidentally, John Fothergill was the first to introduce one of the now famous *Oenotheras*, namely *Oenothera suaveolens* (sweet-scented primrose), into Europe, in 1778 (see de Vries, 1905, p. 215).

<sup>3</sup> His main divisions of the plant kingdom were as follows :—

(a) the *Phanerogams*, or flowering plants, with twenty-three classes; these were the plants with obvious sexual organs;

The *Systema Natura* went through many editions, thus proving that the artificial system of the author had some practical value, at least for those who worked with plants.

Linnaeus began his work convinced that species were immutable, each one being originally created by the Creator. Thus he is credited with the saying "that there are as many species as there were created in the beginning". Even now, more than two hundred years after the publication of his works, we still use the Linnæan species as the common basis of systematics today. With advancing years Linnæus' views matured after he realised the extent of overlapping of varieties and the results of hybridizing plants. Thus his conviction of the immutability of species was lessened; he came to consider that perhaps it was the genera which had been originally created<sup>1</sup> and that new species could arise from old ones. Throughout his botanical career Linnæus was forever on the look-out for a way of expressing a natural system of plant classification. His sexual system he knew to be artificial; a mere convenience. So in his *Philosophia Botanica*, published in 1751, he attempted to formulate a more natural system; thus he was led to distinguish between orders and classes, most of which still stand today. Throughout his life Linnaeus was essentially a deeply religious man; his influence on botany was profound and lasting, although he has been accused of being dogmatic. Nordenskiöld<sup>2</sup> can say of him: "he who has so often been accused of dogmatism was really less dogmatic than many modern scientists who have proved themselves ready to accept blindly the prevailing theories of the day". A modern opinion is given by J. Ramsbottom,<sup>3</sup> who considers that if philosophical considerations are omitted then Linnæus' writings show an up-to-date treatment of the flowering plants. Much of his theorizing is sound also.

Succeeding plant classifiers take us out of the speculative period

<sup>1</sup> Nordenskiöld, 1929, p. 214.

<sup>2</sup> *Ibid.*

<sup>3</sup> 1941, p. 280.

- 
- (b) the *Gryptogams*, or flowerless plants; these have no obvious sexual organs. The latter group included only one class. Classes one to twenty-three of the *Phanerogams* were sub-divided as follows :—

Classes 1-20 were hermaphrodite.

Classes 1-15 were plants with free stamens; the further subdivision depended on the number, length of, and mode of insertion of, the stamens.

Classes 16-19 were plants with the stamens united to each other.

Class 20 comprised those plants with their stamens united to the pistil.

Classes 21-23 were the plants with unisexual flowers.



into the formulative period, but it is convenient at this stage to continue quickly the story of plant classification, considering only the important features.

A. de Jussieu (1748-1836) extended Linnaeus' idea of orders and many of them were quite natural. Thus we have now gone a step further in the formulation of the evolutionary scheme. In fact, in de Jussieu's *Genera Plantarum* of 1789 we find the first attempt to formulate a natural classification. He divides plants into acotyledons, monocotyledons and dicotyledons. This is a grouping which appears to be perfectly natural, and it still stands today.<sup>1</sup>

While in the seventeenth and eighteenth centuries plant classification was making such great headway, the classification of animals was neglected. In the Renaissance period the system of Aristotle was held to. According to Nordenskiöld,<sup>2</sup> this neglect of animals was largely due to the fact that the natural groups of animals are so easily recognised. Aristotle was, therefore, on safe ground when he suggested that man's natural *instinct* could be trusted to distinguish between natural groups, such as those of birds, fishes, etc., for they fall into categories which any one can recognise. To the plant classifiers then, the classification of animals did *not seem to* require urgent attention. On the other hand, the natural groups of plants, according to Nordenskiöld, are not so easily discovered. Long study is first necessary in order to distinguish between them. So man with his passion for classifying things turned his attention more easily to the plants than to the animals.

This explanation of Nordenskiöld of the fact that in this period far more attention was paid to plant classification than to that of the animals may or may not be correct. It is just as obvious to anyone that, say, a moss and a daffodil, fall into different natural groups as, say, a bird and a fish. Actually, before a real classification of animals could be attempted, anatomy and related branches of zoology had to develop first. Thus the investigation of plants

<sup>1</sup> De Jussieu's major grouping of plants is as follows :—

- (1) *Acotyledons*; plants with no cotyledons, comprising the algæ, fungi, bryophyta, pteridophyta and some aquatics.
- (2) *Monocotyledons*; plants with one cotyledon in the seed. These could be further subdivided according to whether they were hypogynous, perigynous or epigynous.
- (3) *Dicotyledons*; plants with two cotyledons in the seed. These could be subdivided according to whether they were apetalous (lacking petals), or monopetalous (with fused petals), or polypetalous (with free petals), or irregulars (of doubtful position).

<sup>2</sup> 1929, p. 198.

was so much easier. Anatomy reached its highest development in the nineteenth century and with it the classification of animals went hand in hand.

Some attention, however, was paid to the animals. Animal classification began with Aristotle (see Chapter 1); this was continued and enlarged upon by Wotton (1492-1555). This process was further continued by Gesner (1516-65) and John Ray (1628-1705). The work of these two men has already been mentioned. Ray's system, which was incomplete, paved the way for Linnæus who, in his *Systema Natura* published in 1735, laid the real foundations of animal classifications. Linnæus divided animals into six classes:—

- |                       |                      |                       |
|-----------------------|----------------------|-----------------------|
| (1) <i>Mammalia</i> , | (2) <i>Aves</i> ,    | (3) <i>Amphibia</i> , |
| (4) <i>Pisces</i> ,   | (5) <i>Insecta</i> , | (6) <i>Vermes</i> .   |

This list, of course, is incomplete, but it still stands today in all essential respects, except for the last group, which included a very heterogeneous assemblage of totally unrelated organisms.

Little advance was made on this classification until Lamarck published his *Zoological Philosophy* and other works (which we will deal with later) and Cuvier (1769-1832) who, in his *Le Règne Animal, distribué après son Organisation*, published in 1816-7, broke away from the Linnean system by refusing to consider divergent characters as of fundamental importance. Instead, he based his classification on types and thus stressed resemblances between animals as being of more importance than differences. Thus he recognised four primary groups—

- |                         |                       |
|-------------------------|-----------------------|
| (1) <i>Vertebrata</i> , | (2) <i>Mollusca</i> , |
| (3) <i>Articulata</i> , | (4) <i>Radiata</i> .  |

The members of each group are united because of a common life-form. The systems of Linnæus, Lamarck and Cuvier, taken together, have thus furnished us with the bases of our modern classifications. Cuvier was in advance of Linnæus, but to him species were immutable. He lived at the time when the idea of evolution was beginning to make headway. To Cuvier, however, evolution was an erroneous doctrine, and through his famous controversy with Geoffroy Saint-Hilaire, which began in 1830, the doctrine was more or less abandoned until the time of Darwin. Nevertheless, Cuvier was the first to recognise that groups of animals were related to each other, not in a straight line fashion, but like the branches of a tree.

*(b) The Speculative Philosophers*

An account of some of the speculative evolutionary writers of the sixteenth and seventeenth centuries is given by Osborn.<sup>1</sup> Among them are found Duret, de Maillet, Diderot, and Oken. Duret (1609) actually describes falling leaves as turning into birds if they happen to fall on land, or into fishes if they happen to fall in water: while de Maillet (1656-1738), in his fantastic book *Telliamed*, describes some remarkable transformations of marine animals into land animals, for instance lions are said to arise from sea-lions, men from mermen. These and such like speculations, or fairy tales, enabled de Maillet to guess at the cause of such changes, and so he arrived at an appreciation of the idea of the inheritance of acquired characters. For instance, a flying fish was accidentally thrown on land and, unable to get back to the water, gradually, in the course of its life time, turned into a bird and, moreover, transmitted the bird condition to its descendants. J. L. A. de Quatrefages (1810-1898), a noted opponent of Darwin, in his book *Charles Darwin et ses précurseurs français* (1892), quotes de Maillet as a French evolutionist worthy of note! De Maupertius considered that material particles contained an essence of living particles, and he based his ideas on the origin of life and its forms on this assumption. As Osborn<sup>2</sup> says: "Here again we find a striking anticipation of our modern doctrine of the course of fortuitous variations" because slight differences in some of these particles in the parents would produce new varieties in the young.

The scholastics, in their philosophy, had concentrated on the idea of "being", but now we have entered the period when "becoming" was the central problem which was beginning to occupy the minds of philosophers. It was natural for the scholastic and later philosophers to take the immutability of species for granted. According to their teachings there was no reason why species should change. As Bishop Hedley,<sup>3</sup> in reference to this point, says of the Patristic school of St. Basil, "They set down, and they undertake to find reasons for it, just as they set down that gold was generated by the sun". As, however, philosophical problems became centred on "becoming" it is quite possible that the whole impetus of the rising tide of scientific investigation and

<sup>1</sup> 1924.

<sup>2</sup> 1924, p. 114.

<sup>3</sup> 1931, p. 17.

speculation may owe its initiating push to this change over of the central problem of philosophy.<sup>1</sup> To question the fixity of species was then a logical step for the naturalists to take.

A prevailing view of generation at this time was that the germ, i.e. the egg or sperm, contained a fully formed but miniature organism. One imaginative observer (Hartsoeker, 1694) went so far as to assert that he had seen a tiny human being in the spermatozoon. This was called the homunculus. The homunculus had but to unfold in order to develop into a human being. This is the doctrine of *encasement*, or preformation, which was called *evolution* by Bonnet and was held in opposition to the epigenetic theory which stated that the germ was homogeneous and that the embryo later differentiated from it step by step, as C. F. Wolff showed in 1759.

This idea of preformation was elaborated by Bonnet into a scientific theory. Previously he had discovered parthenogenesis in the *Aphididae*. Incidentally, this discovery was probably his greatest contribution to science. According to him, every female contained not perhaps a fully formed but small individual, but all the germs of all her descendants. These germs were not necessarily confined to the egg-producing bodies, or ovaries, but they may be scattered over all her body. Clearly these germs recall the monads of Leibnez. The modern idea seems to combine both the theories of preformation according to Bonnet and that of epigenesis. There is no homunculus in the egg or sperm, but its nucleus does seem to contain particles of some unknown constitution (the genes) which in some mysterious way influence development.

The preformation theory of Bonnet enabled him also to work out a theory of descent. He believed that nature was ordained to produce more perfect types. Thus he set forth a continuous sequence

<sup>1</sup> The few examples given above will suffice to show that the Speculative Philosophers were rather wild in their speculations, and in some respects this extravagance retarded the progress of biological thought, by making reputable biologists wary in their statements and advocacy of theories. As Nägeli says: "We might have expected that after the period of the Nature-philosophizers, which in Germany crippled the best forces that might have been used for the advance of the science, we should have learnt something from experience, and carefully guarded the field of real scientific work from philosophical speculation. But the outcome has shown that, in general, the philosophical, philological and æsthetic expression always gets the upper hand and a fundamental and exact treatment of scientific questions remains limited to a small circle" (From T. H. Morgan's *Evolution and Adaptation*, 1903, pp. 452-453). Nevertheless, the fact remains that these speculations played a part in the general synthesis of ideas of organic evolution by putting forward suggestions some of which later bore fruit.

of forms arising in a predetermined manner (because the germs are already present in the females), propelled towards the ultimate goal by some inner cause, and striving to reach the most perfect form of all, namely man. This evolutionary sequence began with the elements of fire, air, water and earth, and proceeded up through plants to fishes, birds, mammals, ending with man. Bonnet did not necessarily hold that this sequence was continuous, forming a chain-like series, for he really thought that there may be several parallel lines of development. Bonnet used the word *échelle* to describe this sequence, while he first used the word *evolution* to describe the development (or unrolling) of the germ into embryo and later adult.

The ideas of Robinet (1735-1820) were rather similar to those of Bonnet in that the aim of nature is to produce the perfect type with man as the present end point. The production of other species of organisms merely represents her unfulfilled strivings or failures in this set purpose. Even man himself may become something more perfect in the future. Here we seem to have a slight hint at the idea of progress coupled with that of a progression of animals from lower stages to higher stages. The idea of progress did not definitely become associated with organic evolution until the late 19th century when rapid industrial developments and the evolutionary theory were advancing together. Bonnet's evolution from the elements air, earth, etc., to Robinet's idea of progression from less to more perfect awaken memories of the early Greek philosophers, and of Aristotle.

Finally we come to Oken (1776-1851), who, strictly speaking, is not in this period, for he died twenty years after Lamarck. Nevertheless he is widely speculative in his biological writings and so it is convenient to consider him at this stage. The cellular structure of both animals and plants was known by this time and many *Infusoria* and other unicellular organisms had been discovered with the aid of the microscope on which improvements were now being carried out. Oken thought that higher organisms were composed of masses of *Infusoria* or infusorian-like bodies, which he called *Urschleim*. Living things, including man, arose from this *Urschleim*; this is a view which recalls that of Anaximander.

These *Urschleim*, or primitive bodies, were considered to be bladder-like and heterogeneous, being made up of an outer skin and containing a liquid matter. Seeing in this liquid matter a substance which present day biologists would call primitive pro-

toplasm, some biologists have been led to consider Oken as the anticipator of the modern cell theory. This theory was really enunciated by Schleiden and Schwann in 1838-39. We will deal with this theory in a later chapter (see pages 100 *et seq.*). It is one of the most important of biological theories and according to it organisms are made up of cells each of which has a certain life of its own but is yet subject to the life of the whole organism. The cell, then, has a certain amount of individuality. Later Dujardin (1801-1862) constituted the infusorians as a separate and distinct group of animal life, while the same man also discovered that protoplasm was always associated with living cells. The ideas of Empedocles and Democritus are recalled by those of Diderot (1713-1784), according to whom the particles composing living things possessed some sort of sensibility and were forever struggling to find a favourable position for themselves. This struggle led to variations among animals.

The cell theory is now one of the foundation stones of modern biology and is closely connected with evolutionary theory and genetics. Although the connection between the first two branches of biology, cytology and evolution, was not recognised for a considerable time, genetics, and its offspring, the chromosome theory of heredity, did not arise until the twentieth century. Of the cell Virchow<sup>1</sup> could say "every animal appears as a sum of vital units, each of which bears in itself the complete characteristics of life". The cell thus came to be regarded as the "unit of life", this is a view which is not so very far removed from the primitive view of Oken. Later, however, it became recognised that the cell is a part of an *organism* which is a composite structure with interdependent parts. The work of later upholders of the theory is summarised by E. B. Wilson,<sup>2</sup> while the modern exponents include the various cytogeneticists such as those of the Morgan school and cytologists like C. D. Darlington<sup>3</sup> in a more specialised book dealing with the nuclear and implied genetical aspects.

(c) *George Louis Leclerc Buffon* (1707-1788)

Buffon was one of the most outstanding naturalists of the eighteenth century. He was also the first naturalist to visualise the

<sup>1</sup> 1855, p. 12.

<sup>2</sup> *The Cell in Development and Heredity*, New York, 1928, several editions.

<sup>3</sup> *Recent Advances in Cytology*, 2nd Ed., 1937.

conception of evolution in a more or less concrete form. Besides his scientific works, which were extensive, he strove to popularize natural science. Singer<sup>1</sup> says of him "he was an attractive writer and perhaps the ablest scientific popularizer that has ever lived". He conceived it to be his main duty in life to compile a history of all cosmology and of plant and animal life. Buffon began the publication of this *Histoire Naturelle* in 1749 when the first book came out. Ultimately the work ran into many volumes; the last one was published in 1804 after his death. Over such a long period of publication his views changed, so that, for instance, whereas he began by supporting the views of his contemporary, Linnæus, he eventually came to oppose and to ridicule his sexual system of classification.

Buffon's biological theories were dealt with in the volume of the history called *Naturelle histoire des animaux*. After hesitating a little he soon came to abandon the idea of the fixity of species, and he did not believe in the creationist theory. In the world of living things he concentrated his attention on observing recurrent characters in organisms, and so was led to the impression that fixed types of animals existed. His views then on this aspect of his belief and teachings are a compromise between the theory of immutability of species and the extreme form of modern evolution which has it that all organisms can be traced back to one common type of ancestor. Osborn<sup>2</sup> remarks: "throughout Buffon's writings we find this wavering between the science of Genesis and the evidence of zoology".

He recognised that the different types of animals could have had different origins at different periods of the earth's history. To account adequately for this he was forced to deny that the age of the earth was about six thousand years. Instead, in order that environment could have had time to act on organisms, he contended that the age of the earth must be much more than this. In a sense he believed in the inheritance of acquired characters, and some modern writers place him along with Lamarck as the co-founder of that causal theory of evolution called "Lamarckism". Throughout all his works Buffon sought to reduce natural events to a mechanical or physical explanation; in this he followed Newton. By considering how vestigial organs are present in organisms, he arrived at the conclusion that some species are degenerate forms

<sup>1</sup> 1911, p. 375.

<sup>2</sup> 1924, p. 133.

of other species. Vestiges, he thought, were merely the remains of organs once useful in a type of animal which had undergone a change in type. From this he could conclude that an ape is a degenerate form of man. He recognised that, bone for bone, the orang-utan was much closer to man than to the monkeys. According to Buffon then man and monkeys were fashioned on a common plan. God made man to the same pattern as He made the monkeys, but into man He breathed a soul.

Buffon also seems to have recognised the occurrence of natural selection, for he considered that there is a continuous struggle between plants and animals in order that nature may retain a certain balance. He modified his views regarding man for he was, of course, aware that he possesses psychical qualities which place him apart from the brute creation—so he considered that man is built up of two qualities, one spiritual and the other material.

In many respects we see that Buffon was in advance of his times, and his works contain many ideas which later became part of the body of doctrine absorbed in the theory of organic evolution. Some of these views are, as we have seen above, his abandonment of the age of the earth as calculated from the Bible, which was a stumbling block to any long term conception of evolution, his ideas of the mutability of species, the changing effect of the environment on species, the inheritance of these changes, his idea of degeneration and the struggle for existence between species, and so on. Thus Nordenskiöld<sup>1</sup> can say of him : " In the purely theoretical sphere he was the foremost biologist of the eighteenth century, the one who possessed the greatest wealth of ideas, of real benefit to subsequent ages and exerting an influence stretching far into the future ".

We can conveniently finish this section with an account of John Hunter (1728-93), the great surgeon, anatomist, naturalist and collector. He was neither a true classifier nor a true speculator; in fact, in many of his statements, especially those on the fossils, he was very cautious. His great life's work was the amassing of the Hunterian Collection in the Museum of the Royal College of Surgeons.

As a naturalist Hunter was quite aware that living organisms never stand alone; every natural thing bears a relation to some other thing, or things; different parts of different organisms are common to each other. Thus, as was usual at this time, he was led

<sup>1</sup> 1929, p. 229.



to consider that some animals had a greater affinity to one another than they had to more unlike animals. He understood the meaning of homology of parts. As he says: "Therefore, in every natural production there is an appearance of affinity in some of the parts of its composition (with those of another natural production); and where there are the greatest number of these affinities or (corresponding) parts, as also the closer the correspondence or affinity between those of one production with those of another, the nearer are those (natural productions) allied".<sup>1</sup>

As an example of his caution we can note his reticence when dealing with the Mosaic account of the Creation. The Bible, he thought, could scarcely be considered as a scientific book. Thus he acknowledges that one must deliberate about nature by starting with the things around one. Nevertheless, Moses' account of the Creation is, according to Hunter, quite classical and even scientific, because in the account of things as they were formed in each of the six days there is discernible a "natural rise or progression from the most imperfect to the most perfect" ending finally in man. Naturalists still clung to the Aristotelian idea of "perfection" in animals, although by this time the "contrarieties" had been abandoned. Hunter's criteria of perfection lay in the number and the disposition of the parts of animals. In perfect forms the parts are distinct and separate from one another, but in the imperfect forms the organs are all jumbled up together; in some cases one part has to perform more than one function, or two different organs may even fuse together.

As a pioneer in comparative anatomy, Hunter maintained that in classifying animals only the great distinguishing features were of value. Thus he founded his Classes on such things as:

- |   |                                  |
|---|----------------------------------|
| (1) heart,  | (2) breathing organs,            |
| (3) brains,   | (4) modes of generation,         |
| (5) modes of coition,                                   | (6) temperature,                 |
| (7) size,   | (8) elements in which they live, |
| (9) essential and circumstantial correlated characters. |                                  |

(Posthumous Papers, p. 25). He believed in some form of progressive and positive evolution, although he did not use this word to describe his meaning. Rather he speaks of the "natural gradation of animals from one to another". By pursuing this natural gradation we are led, at least theoretically, to the original

<sup>1</sup> Posthumous Papers, ed. by J. Owen, 1861.

species, but it would be difficult to do this now starting with any of the existing wild animals. In fact, the origin of species goes back to the very beginning of Time, of which period we can form little idea. "But, I think, we have reason to suppose there was a period of time in which every species of natural production was the same; there then being no variety in any species; but the variations taking place on the surface of the earth, such as the earth and water changing situations, which is obvious; as also the change in the poles or ecliptic, which I think is also obvious".<sup>1</sup>

As a special creationist, Hunter is in doubt here whether species have changed into new species, or varieties have merely arisen as conditions determined, but that some kind of change has occurred through the passage of time he has no doubt whatever. It is interesting to note also how he goes to natural (if rather cataclysmic) environmental changes for the casual factors of the changes occurring in species. Later Lamarck was to use the environmental factor as the chief one causing the evolution of species in his well-developed, if somewhat mystical, system of evolution.

#### (d) *The Natural Philosophers*

While the plant and animal classifiers and the Speculative Writers were at work on their biological problems, the Natural Philosophers, chiefly of the German school, were busy working out their syntheses of ideas on life and on the bases of knowledge. Except for Kant, who began as a man of science, these writers could scarcely be called biologists, nevertheless they endeavoured to give explanations of life and its meaning. Although they were becoming familiar with the various phenomena, such as adaptation, survival of the fittest, etc., they were not evolutionists in the modern sense of the word. They did, however, recognise that change in the world of living things was a fundamental feature. That is, the *idea* of evolution was being gradually formulated. It is due in part to these philosophers that the modern view of historical and phylogenetic evolution was discovered.

The separation of mechanism from vitalism, which was the accomplishment of this school of thought, probably gave *direction* to the *course* of science, because, whether wholly correct or not, it led to the view that natural events were the result of natural causes. The passage to a complete agnostic, or atheistic, materialism

<sup>1</sup> Posthumous Papers, ed. by J. Owen, 1861, p. 4.

was then easy. Earlier views attributed natural events more directly to the Creator as the sufficient Cause. The mechanistic views at first seemed to be diametrically opposed to the vitalistic views, of those people who considered that life and its manifestations were properly to be placed in the domain of religion. An inevitable break occurred which to some extent culminated in the long drawn out controversy over evolution, brought about by the publication of Charles Darwin's *Origin of Species*.

It is unlikely that this evolution of the idea of evolution could have matured so quickly but for the philosophising of the thinkers of the seventeenth and eighteenth centuries.

The first Natural Philosopher of any importance to the theory of evolution was Francis Bacon (1561-1627), who seems to have recognised that variations among species occur in nature. He seems also to have been the first person to contest the idea of the immutability of species. Descartes (1596-1650) was among the first to break way from scholasticism, and to attribute to natural causes the occurrence of natural events, a view leading to the development of a pure form of mechanism. Descartes, however, believed in God. His physics is not to be taken as meaning what we understand by the word today. A knowledge of physics to Descartes did not mean a knowledge of "actually existent Nature". According to him, in order to have full knowledge, one needs to understand metaphysics and physics; and in his metaphysics he shows that the principles of physics can be deduced from this higher branch of knowledge. His natural philosophy is a part of his metaphysical system. In this system he proves that only God depends on no other Being for his existence, thus God is absolutely independent.

Material things exist, but differ from mind; and further, according to Descartes, no kind of intervention is possible between them. It was this differentiation of mind from matter that began the controversy between mechanism and vitalism. In his Natural Philosophy also he tries to prove that the existence and behaviour of material things can be explained mechanically (i.e. mathematically). Living things can differ from dead things only in that the former are much more complex than the latter,<sup>1</sup> for the "body of man is nothing but a statue or machine made of earth". In the last analysis, however, everything depends on God for its existence. Descartes is not an evolutionist, but by his mechanical

<sup>1</sup> *Traité de l'Homme*, AT 11; 120.

views he paved the way for a materialist form of evolution by chance. Without this philosophy it is quite possible that the theory of Evolution developed by the followers of Darwin would never have become materialistic, but would perhaps have remained what this author intended it to be, that is, a theory based on a self-evident axiom, namely, that which cannot live dies.

The next philosopher with whom we are concerned is Leibniz (1646-1716). As a philosopher Leibniz contributed greatly to the development of modern civilization, and he stands out as a defender of vitalism against the Cartesian mechanistic tendencies. He resurrected the old Aristotelian term "entelechy" and used it in his Monadology to account for the vitalistic activity of living things.<sup>1</sup>

As regards evolution Leibniz should be mentioned for his views on preformation, in which he believed, and for his dictum "that nothing happens all at once". This assertion is repeated several times in his works, and it leads logically to his law of continuity. This law states that "Everything goes by degrees and nothing by leaps, and this rule as regards change is part of my law of continuity". Osborn<sup>2</sup> contends that this passage indicates that Leibniz held definite views of the evolution of life, and he quotes him as recognising intermediate forms between organisms. He considered that those intermediate between man and apes may possibly exist in some other world but have been removed from the earth in order to emphasise the superiority of man over the members of the lower creation.

It is doubtful, however, if Leibniz really believed in any distinct form of evolution, much less in the modern idea. Although he says that "nature never makes leaps", in the next line he remarks that no two things are exactly similar, and hence grade gradually and imperceptibly into one another. As Russell<sup>3</sup> remarks: "Why Leibniz held that substances form a continuous series it is difficult to say. He never, so far as I know, offers a shadow of a reason except that such a world seems to him pleasanter than one with gaps".

Finally we come to the most important of the Natural Philosophers. It has been said that Kant has made the greatest contribution to human thought since the time of Socrates. Along

<sup>1</sup> G111.657 D.243 from Russell, 1900, p. 271.

<sup>2</sup> 1924.

<sup>3</sup> 1900, p. 65.

with Descartes, he was primarily responsible for separating the treatment of body and soul. Biology became the study of the mechanical aspects of life, while psychology was reserved for the treatment of mind and soul. Indeed, Kant begins with this separation of body from mind, but at the same time he notes that our knowledge of external things of necessity starts first in the mind. The very first sentence of the introduction to the *Critique of Pure Reason* begins with this recognition. "There can be no doubt," he says, "that all knowledge begins with experience. . . . In the order of time, therefore, we have no knowledge antecedent to experience, and with experience all our knowledge of method begins." But this does not mean to say that all knowledge arises out of experience.<sup>1</sup> Although in the *Critique of Teleological Judgment* Kant, as a biologist, discards the principle of teleology, he is also careful to point out that a mere mechanical explanation of a living thing, being incomplete, is not sufficient. An organism possesses a formulative principle which no mere mechanical object can possess. Thus Kant defines an organism as a natural product<sup>2</sup> "in which every part is reciprocally means and ends". Teleology is excluded from theoretical natural science in order that a study of nature may be restricted to a mathematical and observable principle on which we can make experiments. This mechanical separation of a part of nature from itself in order to facilitate experimental investigation enables Kant to enlarge on his definition of an organism by adding to it:<sup>3</sup> "In it nothing is vain, without purpose, or to be ascribed to a blind mechanism of nature". Thus Hans Driesch<sup>4</sup> can call Kant a dynamic teleologist.

This separation of body and soul and the discarding of teleology in the natural world has probably led to many fruitful experimental results on living things, especially in the domain of physiology, but in theoretical biology it leads naturally and logically to a pure materialistic interpretation in which the necessity for purpose, or for some outside controlling power, is rendered unnecessary. It is, then, but a short step to the complete denial of a Higher Power, or at least to the assertion that this Power is completely disinterested in natural affairs. Man becomes the slave of nature, evolving blindly along a path leading to progress, or perhaps to perdition.

<sup>1</sup> N. Kemp Smith, 1929.

<sup>2</sup> A. D. Lindsay, 1934, p. 258.

<sup>3</sup> *Critique of Judgment*, Pt. 2, Div. 1, Sect. 66, trans. J. H. Bernard, 1914, p. 281.

<sup>4</sup> 1914, p. 87.

The effect of this system of thought on Kant himself was to make him despair, for he tells us that we can never really hope to "understand" living things.<sup>1</sup> "Indeed so certain is it, that we may confidently assert that it is absurd for man even to hope to entertain any thought of so doing, or to hope that maybe another Newton may some day arise to make intelligible to us even the genesis of but a single blade of grass from natural laws that no design has ordered."<sup>2</sup> That statement still stands today. Even if a Newton came an Einstein would have to follow.

Purpose in nature is nevertheless existent and Kant attempts to reconcile mechanism and teleology, although he may conclude that our mental powers are so limited as to be unable to do this. If we do not "understand" a thing then, according to Kant, we cannot know anything about it. He considered that while we can conceive the existence of the soul, free will, even God, we can never *know* anything about them because we cannot hope to "understand" them. This idea of Kant's which led him to restrict man's reasoning faculties to within narrow limits had, however, a great effect on the materialistic way of thinking. It meant that if we could not "understand" any mystical powers, or entities, associated with organisms or phenomena, then we could ignore them. Such a theory is scarcely tenable nowadays. For instance, no one pretends that they *understand* what is really meant by such concepts as, for example, space, energy, or genes. A simple illustration will show the weakness of the Kantian dictum. Meditation on God provides a perfect discipline. It is a high form of prayer. Yet no human being could hope to understand the Creator or His ways. God would not be God if we could. This limitation of objectively valid knowledge to "understanding" in Kant's sense of the word is the basic fallacy of Kant. The very fact that we *can* meditate on God implies that we *know* something of His attributes and of His ways of approach to man.

As we have now seen some of Kant's main principles we are in a position to consider his evolutionary views. The passage quoted below is taken directly from J. H. Bernard's translation of the *Critique of Judgment* and it is worthy of study for it seems to

<sup>1</sup> Kant gives the term "understanding" a rather special meaning. To him a thing is not known unless it is understood, that is, known in such a way that the knowledge is capable of scientific (empirical) demonstration through the application of the categories of understanding to sensible intuitions. Only such knowledge, according to Kant, has objective validity.

<sup>2</sup> *Critique of Reason*, p. 400.

summarise the philosopher's views regarding evolution. It shows that he recognised (a) that a system of reproduction (descent) may be present in nature, (b) that there is a common plan of organisation in animals, (c) that by modification of this plan species are visualised as having arisen, and (d) that this indicates a possible genetic relationship which may help us to give a mechanical explanation to the evolution of the highest organisms. The passage is as follows:—  
“It is praiseworthy by the aid of comparative anatomy to go through the greater creation of organised natures, in order to see whether there may not be in it something similar to a system and also in accordance with the principle of production. For otherwise we should have to be content with the mere principle of judgment (which gives no insight into their production) and, discouraged, to give up all claims to *natural insight* in this field. The agreement of so many genera of animals in a common scheme which appears to be fundamental not only in the structure of their bodies but also in the disposition of their remaining parts—so that with an admirable simplicity of original outline, a great variety of species has been produced by the shortening of one member and the lengthening of another, the involution of this part and the evolution of that—allows a ray of hope, however faint, to penetrate into our minds, that here something may be accomplished by the aid of the principle of the mechanism of nature (without which there can be no natural science in general). This analogy of forms, which with all their differences seem to have been produced according to a common original type, strengthens our suspicions of an actual relationship between them in their production from a common parent, through the gradual approximation of one animal genus to another,—from those in which the principle of purpose seems to be best authenticated, i.e., from man, down to the polyp, and again from this down to mosses and lichens and finally to the lowest stage of nature noticeable by us, viz. to crude matter. And so the Technic of Nature, which is so incomprehensible to us in organized beings that we believe ourselves compelled to think a different principle for it, seems to be derived from matter and its powers according to mechanical laws (like those by which it works in the formation of crystals)”.<sup>1</sup>

Here for the first time in our perusal of those who seem to have had evolutionary inclinations we meet with a clear definite reference

<sup>1</sup> Kant's *Critique of Judgment*, Pt. 2, Append. Sect. 80, pp. 337-338, in J. H. Bernard's trans., 1914; otherwise *Critique of Judgment*, p. 418.

to a *genetic*, or blood, relationship between genera of organisms from man down to polyp, plants and inanimate matter. Although some previous writers have visualised systems giving rise to serial classifications, none up to the time of Kant definitely stated that their series was phylogenetic. The implication of Kant's view is that from an anti-teleological materialistic standpoint man is nothing more than a mere highly evolved animal. Kant, of course, was fully aware of the phenomena of adaptation and of the mutability of species; possibly also he has some vague idea of natural selection. When man is included in the animal kingdom in this way the theory of descent is greatly strengthened because nature is then seen as a unified whole, and the theory of evolution unites a large mass of apparently disconnected facts. As Lindsay says "The test of the theory is not that it fits *the* facts. As Kant says, we are confronted with the *boundless* multiplicity of nature. The test is rather the greater success with which a theory will unite intelligibly a large number of facts."

With Kant the speculative period in the history of evolution closes. The ideas of this period have been most fruitful from the biological point of view. It is a long journey from Gesner's *History of Animals* to Kant's matured views. Logically enough, however, Kant's views merely represent the culmination of the ideas of systematics or classification of organisms worked out so laboriously by the earlier workers like Gesner, Gesalpino, Linnæus, etc. In theoretical as well as in practical biology, it became recognised that species were mutable. The idea of "becoming" replaced that of "being", and so the way was laid open for the entrance of the idea of evolution, or the gradual becoming of new living things from previously slightly different living things. Buffon saw similarities and a common linkage between man and monkeys, but he recognised that the Creator implanted a soul into man. Thus the soul was still the definitive principle. The *idea* of evolution was first recognised as being connected with the phenomenon of change in the organic world. It would never have progressed beyond a mere recognition that change does occur but for the development of two aspects of nature, the mechanical (physical) and the vitalistic (teleological). This conception was, as we have seen, first stated by Descartes, and culminated in Kant's rejection of teleology in the study of natural events. Change could now be expressed as true evolution. This idea was by now firmly established, and Kant, by his insistence on a true



relationship between living things, laid the foundations for the establishment of evolution as a principle. This was only possible by a further separation of mechanistic principles from vitalistic ones. Even Kant recognised that somehow or other these were connected. Thus in modern times teleology has been mistrusted, and the central idea of evolution still remains as the doctrine of descent with modification, itself a direct extension of Kant's views on the subject.

## CHAPTER 3

### THE PERIOD OF FORMULATION FROM 1790 to 1900:

#### (A) THE REAL BEGINNINGS OF EVOLUTIONARY THEORY

##### I. INTRODUCTION: THE REVOLT AGAINST MEDIAEVAL PHILOSOPHY

THE age of evolutionary speculation, if such it can be called, was also the age when far greater advances were made in other scientific pursuits. The Renaissance of science, after the decline in popularity of scholasticism, began about 1600 A.D. The revolt against mediaeval philosophy, however, probably first began with Duns Scotus (about 1265-1308), who stressed once again the clear distinction between theology and philosophy<sup>1</sup> which the latter members of the Order<sup>2</sup> had more or less rejected. Between the time of St. Bonaventure and Scotus the true value of philosophy had been decried by members of the Franciscan Order. Scotus restored it to its proper place. But in order to do this he had to criticise the philosophical systems of his predecessors so drastically that the net result of his work was that he gave a further impetus to the discrediting of philosophy in general. Duns Scotus was followed by William of Occam (d. 1347), who ushered in the period of nominalism. Nominalism certainly taught, along with St. Thomas, that the only realities were individual things. The chief teaching of nominalism, however, is that nothing corresponds in reality to our universal concepts, so that the names by which we signify these concepts are names of convenience only, bearing no relation to reality. Consequently, since all science deals with universals, all science is divorced from reality. As this is obviously absurd, then this conclusion of philosophy weakened its position as a significant method of attaining true knowledge. Men began to distrust the power of human reason and turned more and more to the scientific method now coming to the fore. Thus, by this separation of theology and philosophy and the later apparent

<sup>1</sup> This dualism of Scotus is not to be confused with philosophical dualism according to which the world has a necessary existence independent of God.

<sup>2</sup> Scotus was a Franciscan.

discrediting of philosophy, the new science arose when men could examine things anew and perform experiments on individual objects (the only realities according to the nominalists).

The Renaissance, then, saw the rise of physics, chemistry, physiology and kindred branches of science. In astronomy Copernicus (1473-1543) announced that the sun was the centre of our solar system, an epoch-making discovery, which upset all previous systems and calculations based on them. Later, Galileo (1564-1642) made numerous astronomical discoveries, and during the same period, Kepler (1571-1630) discovered the laws of the movements of the planets. Sir Isaac Newton (1642-1727) enunciated the law of gravitation and, in order to make his system intelligible and usable, he was forced to invent that wonderful tool, the infinitesimal calculus. The chemist Boyle also lived in this period (1627-1691).

Dissections of the human body were possible in the thirteenth century, but human anatomy was still based on the teachings of Galen. Harvey (1578-1657) discovered the fact of, and the path of, the circulation of the blood in human beings. But modern anatomy probably began with Vesalius (1515-1564),<sup>1</sup> rather earlier than Harvey. Malpighi laid the foundation stone of embryology by his description of the development of the chicken in the egg. He was probably the first real embryologist since the time of Aristotle, who, incidentally, also gave us a description of how the chicken develops. Malpighi also described the structure of the lung and showed that the arteries and veins were connected by capillaries. Then followed Leeuwenhoek (1632-1723), who discovered what we now know to be spermatozoa and bacteria, and thus paved the way for the animalculists and later workers on reproduction.

Science was by now definitely established and the new knowledge was speedily added to by a host of later workers. Among these can be mentioned the chemists Black and Priestley (1733-1804), who discovered carbon dioxide and oxygen respectively; the physicist Laplace (1749-1827), who also worked in astronomy; Cavendish (1731-1810), who analysed water; Lavoisier (1743-1794), who unified and developed the work of previous chemists; and Heller, the physiologist and embryologist.

During these years biology, from its evolutionary side, advanced only relatively slowly. The age of speculation in evolution is

<sup>1</sup> Cole (1944, p. 56) calls Vesalius the "father of modern anatomy."

really the age of classification, when plants and animals became better known. Nevertheless, evolution in this period became a definite idea; this was due, however, not to the scientific workers, but to the philosophers, culminating in Kant. The imaginative writers like De Maillet, Diderot and others need not be taken seriously. As Osborn<sup>1</sup> says, "they were either out of date or upon the sidetracks of thought". The Natural Philosophers, as we have seen, were busy synthesising ideas of life. They realised that the naturalist had not yet collected enough evidence, or made a sufficient number of observations of nature, to dare to speculate upon such a fundamental principle as that of genetic evolution. Their realisation of the need of such a unifying principle was implied in the struggle to compile their classifications. Even among the philosophers there was no clear exposition of the idea until we reach Kant, who for the first time, in his *Critique of Judgment*, puts forward, as a definite possibility, the genetic relationship between genera of living things.

After the time of Kant several scientific workers took up the idea. Thus the succeeding period can rightly be called the period of formulation, during which the idea of evolution became known to an increasing number of biologists. So it developed until the philosopher Herbert Spencer published his fully developed cosmic system, and later Charles Darwin and Russell Wallace gave their important contribution to the scientific world. The principle of evolution was thus established, and to many people it soon seemed to be so true as to be described as a fact—"an incontrovertible fact", as Julian Huxley says. Nevertheless, it is not to be thought that up to the time of publication of Darwin's *Origin of Species* there was a *continuous* scientific development of the concept. A few men took up the idea and developed it, men like Erasmus Darwin, and Lamarck and Geoffery St. Hilaire. But the discussion never penetrated to the lecture rooms. As Weismann<sup>2</sup> tells us, in the fifties of last century he and the younger men like him had no idea that there was such a theory. Possibly this was due to a "soft-peddalling" tactic on the part of the teachers and professors of biology who had seen the effects of, and knew all about the works of, the Speculative Naturalists.

The famous controversy between St. Hilaire and Cuvier resulted in the temporary eclipse of investigation on evolutionary lines, at

<sup>1</sup> 1924, p. 107.

<sup>2</sup> 1904, p. 28.

least in France. Hence the balance of opinion was still in favour of special creation for the origin of species; it was not in favour of their gradual origin by transformation. Thus Dampier-Whetham<sup>1</sup> writes: "Indeed it took two thousand years of time, and the labours of many quiet and unphilosophic physiologists and naturalists, to collect enough observational and experimental evidence to make the idea of evolution worth the consideration of men of science. It is a good illustration of the true scientific attitude of suspension of judgment in the face of inconclusive data that naturalists, for the most part, left evolution to the philosophers, and that till Darwin and Wallace published their simultaneous work, the balance of scientific opinion when expressed at all was against the theory."

In this and the succeeding chapter it will be necessary to consider the biological accomplishments and opinions of some of the most outstanding biologists of this period of formulation. We will then be in a position to assess the work of the greatest biological figure of the nineteenth century, namely, Charles Darwin.

## 2. ERASMUS DARWIN (1731-1802)

The first evolutionary naturalist of this period was Dr. Erasmus Darwin, who was the grandfather of Charles Darwin. In many ways he was as famous as the famous originator of the theory called Darwinism. In fact, he seems to have had a very versatile brain, and many of the conclusions he reached, or perceived as indistinct ideas at the back of his mind, have survived him and his grandson. Some of his thoughts still persist today, while the old Darwinism is so modified as to be almost unrecognisable. Hesketh Pearson, a direct descendant of this Darwin, in his biography<sup>2</sup> sums up his life's activities in the sentence, "There is hardly an idea and hardly an invention in the world today that Erasmus Darwin did not father or foresee, from the philosophy of Bernard Shaw to the phonograph of Mr. Thomas Edison, from eugenics and evolution to aeroplanes and submarines, from psycho-analysis to antiseptics."

Erasmus Darwin is of importance to our project in that, hidden in the mass of his writings are several passages that seem to form the bridge between the opinions of Buffon and those of Lamarck.

Many of the thoughts expressed in his books certainly show that

<sup>1</sup> 1930, p. 292.

<sup>2</sup> *Doctor Darwin, A Biography*, London, 1930, Preface, vii.

the author had quite definite ideas about evolution. He did not actually use the word evolution in our sense, for by it he meant the development of an organism. In his book *The Botanic Garden* (1791) he talks of "the gradual *evolution* of the young animal or plant from the egg or seed." He was grasping for a basis or formula on which to build up his ideas, but he never found one. He never came to realise that evolution as an unfolding principle could be used to integrate biological knowledge into a comprehensive whole. He dealt with many concepts but missed that of natural selection. So it was left to his grandson, Charles Darwin, to do this. This is interesting because, besides being a physician, Dr. Darwin was a competent naturalist well acquainted with Malthus' views and the struggle for existence among living things, such as plants. He recognised, too, that this struggle kept down the numbers of organisms, but he did not arrive at the idea of natural selection consequent upon the struggle for existence which seems so obvious to us today. E. Darwin also dwelt upon the effects of the environment on organisms; possibly this is the reason why he did not perceive the operation of natural selection.

Erasmus Darwin was the first poet of science we meet with since the time of Lucretius. His most important poem is the *Temple of Nature*, published in 1802, after his death. A large two volumed work called *Zoonomia, or The Laws of Organic Nature*, was published in 1794-96. These two works contain his most important references to evolution. Thus, as they were published so late they probably represent his matured views about the world of living things. Krause (1879), in his *Kosmos and Life and Study of the Works of Erasmus Darwin* gives us an account of his writings.

As far as his views on evolution and related topics are concerned, Dr. Darwin would seem to occupy a place at the end of the speculative and at the beginning of the formulative periods. He was essentially a man of ideas, yet he was practical. Some of these ideas, however, were merely rather wild speculations, like those of Oken or de Maillet. He continued the work of Buffon, but he did not succeed in formulating any principles. Thus, as was said above, he represents the stepping stone between Buffon and Lamarck. For this reason his work is historically important, and also because in many of his opinions he seems to have pre-dated Lamarck. It is necessary then to treat his contributions to evolutionary science in some detail.

Erasmus Darwin did not accept the preformation theory,

i.e. the theory that the sperm contained a miniature being or homunculus, chiefly on account of the difficulty encountered in trying to imagine that such a small complete being could exist intact in the sperm.<sup>1</sup> Darwin, however, could yet believe that the basic parts of living things were existent in the substance now called protoplasm.<sup>2</sup> In this latter view he approached the modern concept of the germ plasm. Still, however, he clings to the old scholastic view that the male is the chief agent concerned in the production of the embryo. He also gives an analogy with plants by quoting an experiment of Kolreuter, the plant hybridizer, carried out in 1760.<sup>3</sup> In this case the hybrids obtained by crossing *Nicotiana rustica* male with *N. paniculata* female were backcrossed repeatedly for many generations on to the male *paniculata* plant. As Darwin remarks, "they become more and more like the male parent, till at length he (i.e. Kolreuter) obtained plants in no respect different from the *paniculata* male parent, and in no respect like the female *rustica*". The true explanation of this unusual behaviour has not been given, in spite of detailed investigation, chiefly by East.<sup>4</sup>

In the *Temple of Nature* he sets forth his views on the origin of life by rejecting the theory of special creation, and appealing to spontaneous generation for the formation of the lowest organisms at least. In the *Temple of Nature* Darwin states:

"Hence without parents, by spontaneous birth,  
Rise the first specks of animated earth.  
From Nature's womb the plant or insect swims,  
And buds or breathes, with microscopic limbs."<sup>5</sup>

And again:

"Organic life beneath the shoreless waves  
Was born and nurs'd in ocean's pearly caves;  
First forms minute, unseen by spheric glass,  
Move on the mud, or pierce the watery mass;  
These, as successive generations bloom,  
New powers acquire, and larger limbs assume;  
Whence countless groups of vegetation spring,  
And breathing realms of fin, and feet, and wing."<sup>6</sup>

<sup>1</sup> See Ed. Clodd, *Pioneers of Evolution*, Rev. Ed., 1907, p. 20.

<sup>2</sup> *Zoonomia*, Sect. 39, p. 489 and p. 109.

<sup>3</sup> *Zoonomia*, Sect. 39, 2, p. 485.

<sup>4</sup> See Babcock and Clausen, 1927, for an account and bibliography.

<sup>5</sup> Erasmus Darwin, 1803, canto 1, lines 247-250, p. 22.

<sup>6</sup> Erasmus Darwin, 1803, canto 1, lines 295-302, p. 26 et seq.

And so he continues until he reaches man, "who styles himself the image of his God".

Darwin's definite opinion that life has arisen gradually and ascended from simple to higher forms by means of acquired characters is brought out in this and succeeding stanzas of the poem.<sup>1</sup> As regards man himself, he noticed the similarities between him and the monkeys. Man has certain features in common with quadrupeds and his posture is not yet quite erect. Erasmus Darwin follows Buffon in considering that man may have sprung from a single family of monkeys, due apparently to the advantages which accrued from an accidental change in a muscle which enabled the thumb to become opposed to the finger tip. Once acquired, this faculty was increased in succeeding generations. His general view of evolution is also expressed in the preface of the *Zoonomia* as follows: "The Great Creator of all things has infinitely diversified the works of His hands, but has at the same time stamped a certain similitude on the features of nature, that demonstrates to us, that *the whole is one family of one parent.*" And again:<sup>2</sup> "This idea of the gradual formation and improvement of the animal world seems not to have been known to the ancient philosophers. Plato having probably observed the reciprocal generation of inferior animals, such as snails and worms, was of opinion, that mankind with all other animals were originally hermaphrodites during the infancy of the world, and were in process of time separated into male and female."

In the section of Chapter 1 on "Aristotle" it was found necessary to conclude that this ancient naturalist and philosopher was not a true evolutionist. Dr. Darwin knew his ancient writers—this is quite obvious from his own writings—but apparently he was unable to find any views in any part of Aristotle's works which corresponded to his ideas of the evolutionary development of organisms. This, then, supports the conclusion mentioned above.

We now come to one of the most important parts of the beliefs of Erasmus Darwin, i.e. his enunciation of the "inheritance of acquired characters". The passages quoted here show quite conclusively that Dr. Darwin had enunciated definite opinions about this topic before Lamarck had published his theory in the

<sup>1</sup> And see Darwin's *Additional Notes* on Spontaneous Vitality of Microscopic Animals in *Temple of Nature* for a full account of spontaneous generation.

<sup>2</sup> *Zoonomia*, Vol. 1, Sect. 39, 4, p. 508.



*Zoological Philosophy*. These views are chiefly put forward in the *Zoonomia* in the chapter on "Generation". In this chapter he puts forward his belief in the descent of organisms by modification of one living filament which the Creator endowed with life and to which He gave an inherent power to respond to its own activities. He says:<sup>1</sup> "From thus meditating upon the minute portion of time in which many of the above changes have been produced, would it be too bold to imagine, that all warm-blooded animals have arisen from the one living filament, which the *Great First Cause* imbued with animality, with the power of acquiring new parts, attuned with new propensities, directed by irritations, sensations, volitions and associations, and thus possessing the faculty of continuing to improve by its own inherent activity, and of delivering down these improvements by generation to posterity world without end?" The following passage, while showing us Darwin's views as to the method whereby living things acquired their adaptations to their environments, also gives us an outline of his evolutionary views from a single living filament. "When we revolve first the changes which we see naturally produced in animals, after their birth, as in the butterfly with painted wings from the crawling caterpillar, or the frog from the tadpole; secondly the changes by artificial cultivation, as in the horses exercised for strength and swiftness, or dogs for strength, courage, or acuteness of smell, or swiftness; thirdly the changes produced by climate, the sheep of warm climates covered with hair instead of wool, and the hare and partridge which are long buried in the snow becoming white during the winter months; fourthly the changes produced before birth by crossing or mutilation; fifthly the similarity of structure in all warm-blooded animals, including mankind, one is led to conclude that they have alike been produced from a similar living filament."<sup>2</sup>

This name "a living filament" is mentioned over and over again in the *Zoonomia*, but Darwin never seems to define it, he never explains what he means by it.<sup>3</sup> According to Osborn<sup>4</sup> he meant what we would call a small mass of primeval protoplasm; while according to Singer<sup>5</sup> he meant a spermatozoon. In any case,

<sup>1</sup> *Zoonomia*, Vol. 1, Sect. 39, 4.

<sup>2</sup> Quoted from C. Singer, 1941, p. 376.

<sup>3</sup> A few references to this name are given in *Zoonomia*, Vol. 1, Sect. 39, 3, p. 489; Sect. 39, 4, pp. 492, 298, 299 and p. 507, where it is applied to plants.

<sup>4</sup> 1924, p. 147.

<sup>5</sup> 1941, p. 376.

it was intended to convey the idea of a unit particle producing living things by generation. Possibly it was allegorized in the Biblical account of the formation of Eve from a rib of Adam.<sup>1</sup> This living filament can be excited by stimuli so as to alter its form and this causes new kinds of sensibility to arise in it and thus induce new changes in the organism concerned.<sup>2</sup>

Thus animals have a similar organisation because they all arise from this single living filament, but as they are endowed with different kinds of susceptibilities and irritabilities, change can take place producing new organisms, for, "just as chemicals combine to give new substances with new properties so an addition of a new part to an embryo gives a new animal".<sup>3</sup> Animals, then, can change or evolve by acquiring new features, by developing some new power which they need and which is called forth in consequence of their wishes, or dislikes, of their pleasures, of their pains, or of their associations. These new acquirements are passed on to their descendants in some cases. In other words, in conjunction with an external stimulus and the inherent activities of the organism concerned, a new inherited character may be formed. Darwin gives examples of how this is done, and of the stimuli producing the changes. For instance, (a) the wants of animals which, in the case of males may be expressed by a desire for possession of the females, may lead to the acquirement of new offensive weapons; (b) feeding habits may change and so lead to changes in bodily features as in the nose of swine adapted for pushing in the loose earth, or in the trunk of the elephant adapted for reaching leaves in the upper branches of trees; (c) the need for security seems to have led to the development of protective colourings, to the development of wings in the place of legs, and to the development of hard shells in certain animals. And so on.

In all these cases the character which was once new and acquired is passed on from generation to generation. "Fifthly, from their first rudiment, or primordium, to the termination of their lives, all animals undergo perpetual transformations; which are in part produced by their own exertions in consequence of their desire and aversions, of their pleasures and their pains or of irritations, or of associations, and many of these acquired forms or propensities

<sup>1</sup> *Zoonomia*, Vol. 1, Sect. 39, p. 489.

<sup>2</sup> *Ibid.*, Vol. 1, Sect. 39, 4, pp. 492-3.

<sup>3</sup> *Ibid.*, Vol. 1, Sect. 39, 4, p. 499.

are transmitted to their posterity."<sup>1</sup> Man also is included in this scheme of evolution. "Now as labour strengthens the muscles employed, and increase their bulk, it would seem that a few generations of labour, or of indolence, may in this respect change the form and temperament of the body."<sup>2</sup>

Here, then, Erasmus Darwin points out the effects of use and disuse in modifying the form of an organism; this is also one of Lamarck's tenets. Indeed, it is strange how closely Lamarck and Dr. Darwin agree in their ideas. Lamarckism could equally well have been called *Erasmusism*. It is possible that, just as in the case of Charles Darwin and Alfred Russell Wallace, here also we have two men working independently and evolving a similar theory of the inheritance of acquired characters. Osborn discusses how this came about, and he decided against the earlier suggestion of Charles Darwin that Lamarck was really familiar with the earlier work (by seven years) of Erasmus Darwin. In many respects also Dr. Darwin puts forward ideas which were accepted by his grandson, Charles Darwin.

### 3. LAMARCK AND LAMARCKISM

Previous to Erasmus Darwin the concept of evolution had been perceived by some individuals, who toyed with it, but yet had reached no definite conclusion about it, with the exception of the philosopher Kant. Dr. Darwin changed all this. By building on the work of his predecessors and adding his own ideas, he attempted to put forward evolution as a definite fact, as the way by which the Creator intended organisms to change and develop. He did more than this, for he tried to formulate a theory of the *cause* of evolution. The evidence that Dr. Darwin held these views is found in scattered passages of his rather wordy writings. Nevertheless, he just failed to produce a completely worked out theory of evolution. This was done a few years after the publication of the *Zoonomia* by Jean Baptiste de Lamarck (1744-1829). As Packard in his biography of Lamarck contends (1901), Lamarck should rank as the first real evolutionist with a complete theory. Although Lamarck put forward many of the ideas of Darwin, he is not, however, a plagiarist. This can be seen readily enough by

<sup>1</sup> *Zoonomia*, Sect. 39, 4, p. 502.

<sup>2</sup> *Zoonomia*, Vol. 1, Sect. 31, p. 356.

anyone who takes the trouble to read the chief writings of both authors, for Lamarck's theory is fully developed and complete in itself.<sup>1</sup>

In his very first paragraph of the *Zoological Philosophy* Lamarck tells us that he set himself the task of the creation of a philosophical system of zoology setting forth rules and principles which could be of general application. It is necessary now for our purpose to examine this book because, in spite of tremendous opposition from all and sundry, Lamarckism still holds sway as a causal theory of evolution.

In some respects Lamarck echoes Aristotle, for example, his theory is built up on the supposition that animals strive towards perfection. Some animals are less perfect than others and the state of their perfection can be recognised by the complexity of their organisation as a body. Thus, Lamarck immediately gets to the root of his problem by recognising that the organ develops first and determines the function. As Hugh Elliott tells us, Lamarck's chief aim in his book was to attack the doctrine of the immutability of species. According to Lamarck the environment has a great effect on species and causes them to change. Species then cannot remain fixed, given a changing environment. By examination of a scale of animals passing from the most imperfect to the most perfect he was struck by the gradually increasing complexity of organisation, and he had to conclude that nature had produced these different forms successively from the worm upwards. "With regard to living bodies, it is no longer possible to doubt that nature has done everything little by little and successively".<sup>2</sup> Lamarck, then, definitely recognised an evolution of species in time and space, and so he was led to consider that the biologist's creation of species, genera, families, orders, and classes was just artificial. These divisions have no real meaning in the natural world, for, as the natural world is made up of individuals which succeed one another without break, it is only the limitations of man's knowledge which causes him to see these divisions in nature.

He defines a species as "any collection of individuals which were

<sup>1</sup> In this account of Lamarck full use has been made of the excellent biography of Lamarck by A. S. Packard (London, 1901), and of Hugh Elliott's translation of the *Philosophie Zoologique* (London, 1914). Material has been collected from scattered sources, but these two books proved to be most helpful. Quotations, unless otherwise stated, are from Elliott's translation, abbreviated to E., followed by the page number.

<sup>2</sup> E., p. 11.

produced by others similar to themselves".<sup>1</sup> Such a definition is exact. If all such species were known then there would be no lines of demarcation between them. As knowledge of species advances he finds that this is so, and often then it seems that the species are delimited one from the other by very small distinguishing but unimportant characters. Lamarck was careful to point out that the question of the mutability of species could have no derogatory effect on religious beliefs. Perhaps the Creator willed it that way.

Hence, species are connected with one another, not in a reticulate or branching fashion, but in a simple linear way. Classification is purely arbitrary and artificial, but it is convenient, for it enables biologists to draw up an arrangement of animals, which will approximate to the natural linear order in nature. Nature has set certain affinities between animals and it is by recognising these affinities that we can create a natural classification. A classification of this kind is necessary to the biologist if he is to form any philosophy of zoology; otherwise the science would be a mere jumble of numerous species. As examples of the use of this natural classification based on natural affinities Lamarck was able to separate *Infusorians* from *Polypes*, *Radiarians* from *Polypes*, *Medusæ* from *Mollusca*, and so on.

As our knowledge of affinities increases so will our arrangement of animals become less and less arbitrary. In order to arrange animals in an artificial system, which will resemble the true arrangement in nature Lamarck makes use of the principle of affinities between them. This, he finds, is expressed in the animal, not necessarily by a resemblance of outward form, but by the resemblance of their essential organs. As he says, organs by themselves do not show an evolution (or degradation) but only the systems of essential organs. Lamarck explains the fact that in some animals some of their organs are in a high state of development while others are in a more or less primitive state by saying that these latter are the organs which are less essential to the organism concerned, and they are the ones which are most subject to change due to the action of the environment. The presence of essential and inessential organs in animals tends to produce such a diversity of species as to interfere with the true linear arrangement, thus producing side branches. The essential systems in order of importance are as follows:—  
(a) nervous system, (b) respiratory system, (c) circulatory systems.

<sup>1</sup> E., p. 35.

The true scale of affinities is recognisable only in the larger groups and not in the smaller ones, such as species, for these are the most subject to the action of the environment which produces variations or anomalies in them which are unrelated to the essential organisation of the animal.

Aristotle had recognised that animals could be divided into two main groups according as they possessed blood or not. Lamarck, while finding also that there are two main groups, considered that Aristotle's criterion was in the opposite direction to the order of nature, and so, in 1794 in his lectures, he proposed the two fundamental divisions of *Invertebrata* and *Vertebrata*. The possession of a skeleton, or vertebral column, at once puts an animal possessing it on a certain level of organisation more complex (and hence more perfect), and completely different from the plane of organisation of animals lacking a backbone. This division also helps us to determine to what state of perfection any given animal belongs. For instance, since man has a vertebral column, and since he is obviously the most perfect organism, then any animal possessing a vertebral column has a more perfect organisation than any animal lacking one.

Linnæus had divided animals according to their complexity as follows:—

- |              |              |                            |
|--------------|--------------|----------------------------|
| (1) mammals, | (2) birds,   | (3) amphibians (reptiles), |
| (4) fishes,  | (5) insects, | (6) worms.                 |

The first four of these correspond to Aristotle's blooded animals, while the last two comprise his bloodless group. Hence, as regards the last two classes, Linnæus' classification was little better than that of Aristotle. What it amounted to was that if any animal lacked blood and did not possess a jointed body then it was classed as a worm. It was unavoidable, therefore, that the class *Vermes* should come to contain a large assembly of totally different animals. Lamarck's recognition and rectification of this weakness of Linnæus' classification was probably one of his greatest achievements. The class *Vermes* corresponds with Lamarck's class *Invertebrata* and, by his use of the ideas of perfection of organisation, he was able to establish a basic system of classification. Modern classifications are merely developments of this. A synopsis of Lamarck's classification is given in the appendix.

There is a close similarity between Aristotle's series of animals and Lamarck's classification of them. This is because both of

them are based on the idea of perfection, which animals strive to reach. These two naturalists, however, differ widely in their interpretation of the inner meaning of series such as these. To Aristotle a series meant nothing more than a table, a convenient arrangement; to Lamarck it meant that in nature there exists a definite linear order among the animals showing it. Species were mutable and changed gradually one into the other. That is, Lamarck meant his classification to show that an evolution of species occurred, while Aristotle was really concerned only with showing that the idea of perfection could be identified with an entelechy.

Lamarck's dichotomy of vertebrates and invertebrates did not begin there. He recognised that all things could be divided into organic and inorganic. Organic bodies are those that are alive, and for the study of them Lamarck (along with Treviranus) proposed the name of *Biology* (1802). Living bodies die and by the decomposition of their parts inorganic substances are produced. Organic bodies are likewise divisible into two groups—plants and animals—and, again, just like Aristotle, he considered the main difference between them to be one of irritability; they also differ in their modes of digestion and locomotion.

In his physiology Lamarck approaches the mechanistic attitude. Thus he says: "The ancient philosophers felt the necessity for a special exciting cause of organic movement, but not having sufficiently studied nature, they sought it beyond her; they imagined a vital principle, a perishable soul for animals, and even attributed the same to plants; thus in place of positive knowledge which they could not attain from want of observations, they created mere words to which are attributed only vague and unreal ideas".<sup>1</sup> In spite of this tendency to mechanism, however, Lamarck did not deny the existence of the human soul. He is emphatic in his protestations of the work of the Sublime Author. Neither did he fall into the error of the later mechanists who imagine that, because some physico-chemical change accompanies a bodily movement or change, then the whole process is explained, or that the physico-chemical change causes the somatic change. According to Lamarck, Richerand defined life as a "collection of phenomena which succeed one another for a limited period in organised bodies". But, says Lamarck, Richerand should have said that "life is a phenomenon which gives rise to a collection of other phenomena, etc., for it is not these other phenomena that constitute

<sup>1</sup> E., p. 212.

life, but they are themselves caused by life". And again, "A study of the phenomena resulting from the existence of life in a body provides no definition of life, and shows nothing more than objects that life itself has produced."<sup>1</sup>

As a scientific worker Lamarck realised that he could not in the nature of things discuss, let alone discover, anything about the human soul, or its connection with the body. As a scientist, however, he considered that it was enough to acknowledge the actual existence of the human immortal soul.<sup>2</sup> To him life comprised the unified working of three parts—the solid, the liquid and the exciting cause of organic movement. This exciting cause was itself made up of electricity and caloric which further possessed a fluid nature permeating to every part of the organism. In the sense that Lamarck meant, it is difficult to see how he failed to realise that there was little difference between this mysterious stimulus to movement and other vital entities such as souls.

Thus did Lamarck bring forward his evolutionary views. Species to him were never constant, they were continually striving to become more and more complex. Indeed this tendency towards complexity is innate in organisms, and furnished Lamarck with the starting point for the development of his whole evolutionary edifice. In his view of life itself this tendency is expressed as the exciting cause of movement made up of caloric and electricity. Due to this tendency living things, having once been spontaneously generated, proceed to evolve in a straight line. But, in fact, as Lamarck proceeded along this line he discerned many exceptions and anomalies. From his view regarding essential and inessential organs, he developed the idea that the environment had a much greater effect on the latter than on the former which determined the organisation of the animal. Thus he was led to place a great emphasis on the action of the environment on organisms in general. This naturally led to his conception of the second great causal agent in evolution, namely, *the inheritance of acquired characters*, as it is called nowadays. We must now devote some time to this important section of this zoologist's doctrine.<sup>3</sup>

To begin with, Lamarck seems to have had an idea of natural selection in that he recognised that there was over-production among species, especially among the lower ones, and their numbers

<sup>1</sup> Both E., p. 201.

<sup>2</sup> E., p. 296.

<sup>3</sup> Neo-Lamarckism will be dealt with in a later chapter.



were kept down by their greater mortality. Animals eat each other, and "we know that it is the stronger and the better equipped that eat the weaker, that the larger species devour the smaller".<sup>1</sup> This struggle extends even up to man, who, because of his passions, keeps down his numbers by warring among his own kind. If we grant glimmerings of the idea of natural selection to earlier writers because of holding similar views, surely we can grant them also to Lamarck. His translator, Hugh Elliott, however, disagrees with this emphatically when he says "Of Natural selection Lamarck had not the slightest conception".<sup>2</sup> In any case Lamarck never applied the idea of this struggle among animals to his theory of evolution; apparently to him its weeding out effect was of no importance.

Organisms live continuously in some kind of surroundings so that the environment is always working on them. The effects produced by the environment are not commonly noticed because it takes such a long period of time before the results can be discerned. Thus the "environment affects the shape and organisation of animals".<sup>3</sup> Changing surroundings produce changes in the animal but not, of course, directly so, for changes in the conditions of life lead to changes in the needs of the animal, and this of necessity leads to a change in its activities. If these new needs become permanent the animal naturally acquires new habits. These habits "last as long as the need that evolved them".

The new activities of the animal lead it to use one part of its body more than another and also to the disuse of some other parts. Such parts which are now no longer needed gradually get less and less in size in succeeding generations until, finally, they disappear.

The environment also affects the parts of plants in a similar way but, as plants can scarcely be said to develop habits, then the changes in the plant body are brought about by changes in its nutrition and in the availability of light and moisture etc. To Lamarck the effect of the environment on organisms seems to be very plain and nature teemed with examples. It was well known in his time that alteration in the environment caused changes in the outward appearance of animals, such as size, colour, shape, etc. Man himself has brought about such changes in his domesticated plants

<sup>1</sup> E., p. 54.

<sup>2</sup> E., Intro., p. xxxiii.

<sup>3</sup> E., p. 107.

such as wheat, cabbages, lettuces and so on, and in his domesticated animals such as pigeons, fowls and dogs.

From observations like these Lamarck then deduced two laws. These are<sup>1</sup>:—

*First Law.*

*By continued use of an organ in animals it becomes greatly strengthened, and enlarged to an extent which is proportional to the amount of its use. On the other hand, by continued disuse of an organ it becomes weaker and deteriorates, finally disappearing.*

*Second Law.*

*An animal thus acquires modifications in response to the environment and all the modifications, providing they are present in both male and female, are passed on by reproduction.*

The first law then includes the effects of use and disuse, while the second one is concerned with the inheritance of acquired characters. It is this second part which has led to so much controversy. Many of Lamarck's opponents do not even seem to have read his enunciation of these two laws, for some of them give the following illustration as showing that use has no effect on inheritance. In China, female children have had their feet encased in tightly fitting shoes from time immemorial but this has had no effect on the size of the feet of their descendants. Lamarck distinctly said that both sexes had to be involved in the process. He could scarcely be expected to know that, in fact, there are two kinds of variations—(a) variations, strictly speaking, which arise in the organisms and are inherited, but which do not seem to be due to the action of the environment, and (b) variations which are caused by the environment but which are not inherited. These latter kind are usually called modifications.

It never seems to have occurred to Lamarck to test his views experimentally and find out whether or not the variations were really inherited. Like Darwin, later, he took inheritance for granted, and instead of experimental evidence he brought forward rather fanciful illustrations of his laws. As examples of disuse he gives the following:—some animals swallow their food without chewing it and so their teeth are not used and now they remain undeveloped in the jaw, or have even disappeared entirely. In the case of the Right Whale M. Geoffréy discovered rudimentary teeth in the jaws of the foetus, while in the case of birds only the

E., p. 113, paraphrased.

groove remains. The ant-eater likewise has lost its teeth through disuse. Certain animals live in caves or in the dark for different periods and so do not need eyes. It is seen that some of them, such as the mole, have small eyes, others, like *Spalax* and *Proteus* have only vestiges left. Molluscs possess a mantle and so eyes to them would be useless, thus they are not developed, although, according to their level of organisation, they should possess them. Snakes do not need legs although in their plan of organisation they should possess two pairs. Snakes have to pass through narrow places continually, and hence to them legs would be useless, if not an actual hindrance. Constant disuse has thus led to their disappearance. Lamarck even gives an example from human beings by citing the case of the great drinkers whose stomachs and intestines are said to be greatly shortened due to lack of use in digesting solid food.

Some of the examples of the effect of constant use of an organ are given below:—water birds by constant stretching of the skin of their feet in skimming the surface of the water and in swimming have gradually developed webbed feet. Clasping birds through constant perching on branches have developed long, sharp and curved digits on their feet. Waterside birds have acquired long necks in an endeavour to catch fish, and also by constantly endeavouring to keep their bodies out of the water they have acquired long legs. Animals, such as elephants, rhinoceroses, oxen, buffaloes and horses, have developed large, heavy bodies through constant browsing on grass and consumption of large quantities of food which caused distention of their organs. The body of the ruminants has become slender and their legs finer through constant exertions in running to escape the attacks of preying animals. The neck of the giraffe has become greatly enlarged because this animal has constantly sought for the uppermost leaves of trees. And so on.

In conclusion, Lamarck sums up by stating : " Everything then combines to prove my statement, namely: that it is not the shape either of the body or its parts which gives rise to the habits of animals and their mode of life; but that it is, on the contrary, the habit, mode of life, and all the other influences of the environment which have in course of time built up the shape of the body and of the parts of the animals. With new shapes, new faculties have been acquired, and little by little nature has succeeded in fashioning animals such as we actually see them ".<sup>1</sup> To Lamarck this is the most important conclusion in natural history.

<sup>1</sup> E., p. 127.

Although Lamarck was thus able to give a reason and, indeed, one which seemed so full of common sense appeal, for the presence of many characters in animals yet his theory was not widely accepted by his contemporaries. The chief reasons for this may have been:— (1) because of a mystical content in his theory whereby an innate tendency seemed to be pushing animals towards greater and greater complexity or perfection<sup>1</sup>. In the use and disuse theory this was expressed as a striving of the animal towards its goal under the influence of the environment. (2) The examples Lamarck chose to illustrate his thesis of use and disuse were, in many cases, rather ludicrous and probably tended to make his contemporaries laugh at the whole theory. (3) Lamarck's views were condemned by Cuvier, who was the most influential biologist of his time. Cuvier's opinion would undoubtedly sway many who might otherwise have been inclined towards Lamarckism.

The whole of Lamarck's theory turns on the question of whether or not acquired characters are inherited. To the author of the theory there was never any doubt about this, and, so far as knowledge went at the time, there was no reason why he should have doubted it. Since his time, however, the theory has been exhaustively examined by experiment but, few, if any proven cases of the inheritance of acquired characters have come to light, cases about which everyone could agree. This does not necessarily disprove the theory. In a later chapter we shall have to examine the evidence for this theory in more detail because it is one of the chief modern theories of evolution.

Lamarck died in 1829. As a biologist he stands out as one of the greatest men of his time; his contributions to systematic zoology alone entitle him to the greatest respect. He was the real founder of evolutionary theory, and by his theory of the inheritance of acquired characters he founded a school which will long have its adherents. He was a botanist before becoming a zoologist, and he was well acquainted with meteorology, physical science, geology and invertebrate palæontology. When he took over the professorship at the Paris Museum of Natural History, he found that the classification of the lowly backboneless animals was in a chaotic state. By his profound researches on these animals, before he died, he brought order out of chaos and established several new fundamental groups—no mean achievement for one man. Probably

<sup>1</sup> Radl, 1930, p. 271, remarks: "Darwin himself only saw in Lamarck's teaching vitalism under a somewhat thin disguise".

because he was constantly using lens and microscope his eyesight gradually failed until he became blind some ten years before his death.<sup>1</sup>

In spite of this infirmity, he continued to work and, by his dictation to his daughter Cornélie, he managed to complete his work before he died in 1829. He was buried in a common grave, but Packard eulogises him as follows: "The life work of Lamarck and his theory of organic evolution, as well as the lessons of his simple and noble character, are more durable and lasting than any monument of stone or brass. His name will never be forgotten either by his own countrymen or by the world of science and philosophy. After the lapse of nearly a hundred years, and in this first year of the twentieth century, his views have taken root and flourished with a surprising strength and vigour, and his name is pre-eminent among the naturalists of his time."<sup>2</sup>

<sup>1</sup> Packard, 1901, quoting Duval, p. 51.

<sup>2</sup> Packard, 1901, p. 61.

## CHAPTER 4

### THE FORMULATIVE PERIOD CONTINUED :

#### (B) FURTHER DEVELOPMENTS AND SOME SIDE ISSUES

##### 1. THE GROWTH OF IDEAS IN BIOLOGY

**A**FTER Lamarck we come to a period in the history of evolution when, with the increase in knowledge in the whole biological field, men were beginning to feel the need of a new cosmogony. The old one, embodied in the theory of special creation, and cramped by the limitations of a literal interpretation of the Mosaic account of the Creation, was not conducive to the further advancement of science, especially biological science. New generalizations were badly needed to weld together the facts and observations of science and the thoughts of men on biological topics. Lamarck's bold conceptions were unsatisfactory in spite of the popular appeal of the theory of the inheritance of acquired characters. Besides, Lamarck was laughed out of court by Cuvier, the "dictator of biology".

Later, in 1844, the famous *Vestiges of the Natural History of Creation* was published anonymously. This book has been decried and laughed at, and yet it ran through twelve editions, the last one of which came out long after the publication of Darwin's *Origin of Species*. In the introduction to the twelfth edition, Mr. Ireland acknowledges that the author was the writer Robert Chambers (1802-1871). After its publication a storm of criticism of all kinds arose. Chambers set out to find the operation of a universal law in the organic and inorganic worlds, and in the process he attacks the prevalent idea of special creation and the immutability of species. Geological history and the order of fossils in the rocks led him to believe that "Time and a succession of forms in gradation and affinity become elements in the idea of organic creation".<sup>1</sup> He then proceeds to draw an analogy between "development" (that is, what we call evolution) and the facts of embryonic growth

<sup>1</sup> 11th Edition, p. 129.

of animals. In fact, he only just misses the idea of "ontogeny recapitulates phylogeny", which was later so elaborately advocated by Haeckel as the biogenetic law.

Thus his studies led him to the conclusion that there has been an evolution of species brought about by the operation of natural laws. Nature indeed is ruled by a universal law which is a fact of great importance. The following passage puts Chambers' evolutionary views in a compact form: "The Creator, then, is seen to have formed our earth, and effected upon it a long and complicated series of changes, in the same manner in which we find that he conducts the affairs of nature before our living eyes: that is, *in the manner of natural law*. This is no rash or unauthorised affirmation. It is what we deduce from the calculations of a Newton and a Laplace, on the one hand; and from the industrious observations of facts by a Murchison and a Lyell on the other. It is a point of stupendous importance in human knowledge; here at once is the whole region of the inorganic taken out of the domain of marvel, and placed under an idea of divine regulation which we may endlessly admire and trust in."<sup>1</sup> Chambers' book was, in fact, the only complete evolutionary one between Lamarck's *Zoological Philosophy* and Darwin's *Origin of Species*. Yet, in spite of its popularity, it was not taken seriously, at least by naturalists, possibly on account of the fact that the author was not a *bona fide* naturalist, and because he points out that naturalists themselves could scarcely be expected to arrive at a universal doctrine like that embodied in the doctrine of evolution. Nevertheless, because his book was widely read and criticized, it must undoubtedly, at least in English-speaking countries, have prepared the way for Darwin's book, perhaps to a far greater extent than is usually admitted. We can say, therefore, that in the early and middle nineteenth century, the numbers of those who gave up the idea of the immutability of species and of special creation increased slowly but surely in all branches of biological endeavour.

In 1802 Reinhold Treviranus (1776-1837) introduced the word *biology* as the science of living things in his *Biologie oder Philosophie der Lebenden Natur* (1802-1805). The introduction of this word at this period was probably timely, for it became recognised that there is a living and a non-living world which are separate and distinct fields for investigation. According to Osborn,<sup>2</sup> Treviranus

<sup>1</sup> 11th Ed., p. 102.

<sup>2</sup> 1924, p. 188.

was not original in his views, for he was essentially a compiler of the ideas of Buffon, Kant and Schelling. The introduction of this word *biology* also served to remind biologists that living things were *wholes* and not just pieces of living matter stuck together as if by glue, like the infusorian masses of Oken. In spite of this, however, in the first few decades of the nineteenth century naturalists were still seeking for artificial affinities between organisms, each one according to the particular aspect of biology with which he was most acquainted. For instance, C. Stewart<sup>1</sup> tells us that we can only build up a natural arrangement of natural bodies on obvious characters which must be external and belong to the body of the organism concerned as distinct and peculiar characters. Such characters as these comprise the form, the number, the position and also the proportions of the parts. Internal parts are not obvious and sometimes are difficult to see and, therefore, are of no value as systematic characters. Cuvier was the first to break away seriously from this slavish habit of the morphologists when he tackled the problems of comparative anatomy. This was the period also when palæontology as a separate study became established by Richard Owen (1804-92). Sir Charles Lyell (1797-1875) published his *Principles of Geology* in 1830. This was a book which laid the foundations of modern geology. Thus it was that the various aspects of natural history were formed into distinct compartments.

The study of classificatory systems became *Systematics* when de Candolle, a botanist, introduced the word *taxonomy* about 1813. Embryology, under Louis Agassiz and von Baer, was developing fast at this time, while in 1817 Goethe introduced the word morphology into science. Finally, chemistry and physics began to be applied to the study of living things. So that gradually physiology developed as that branch of the subject which attempts to give descriptions of organisms as far as possible in physico-chemical terms.

## 2. TRANSFORMATION IMMEDIATELY FOLLOWING LAMARCK

### (a) Johann Wolfgang von Goethe (1748-1832)

During these early years of the nineteenth century the poet Goethe published his ideas on the homologies of the parts of plants. In his *Metamorphosis of Plants* he advanced the theory that the

<sup>1</sup> 1817, Sect. 16, p. 3.



various parts of the flower, i.e. the sepals, petals, stamens, etc., were extreme modifications of ordinary leaves. His attention then turned to animals; by a study of their structure he was led to formulate his "unity of type" theory in which he recognised that such groups as families, orders, etc., were mere variants of a limited number of plans underlying them all. Ultimately the parts of animals could be referred to one animal model. This is Goethe's *Bildung und Umbildung* theory. This idea of unity of type among organisms was popular at the time, but Goethe embellished it elaborately.

The "laws" of Goethe, coupled with Linnæus' discovery of sex organs in flowers, have been said to be real stepping stones in the development of the evolutionary concept. Haeckel was a firm believer in Goethe as an expounder of evolution by descent and quotes him as follows: "This much then we have gained; that we may fearlessly affirm without hesitation, that all the more perfect organic natures, such as fishes, amphibious animals, birds, mammals and man at the head of the list, were all formed upon one original type which varies only more or less in parts which are none the less permanent, and which daily changes and modifies its form by propagation". Oscar Schmidt<sup>1</sup> tells us that Goethe's archetype made it impossible for nature to deviate from the central plan of her Creator.

But where in the works of Goethe is there an account of the actual transformation of one existing *species* into another *species*? The passage quoted above may show that he believed that phyla were distinct groups each cut off from the others, for each is perfect in its own way. Change apparently may take place within the phylum; this is a kind of mitigated evolution as Dorlodot<sup>2</sup> calls it. Quite possibly Goethe really believed that species were immutable. In Goethe's theory of evolution, if such it can be called, we have really a theory of modification of the *expression* of the archetype, and not of the evolution of any single species, for each of these must conform to the pattern set by the archetype. His ideas in this respect, then, seem to be rather vague and unsatisfying as if he were striving to reduce living things to a common denominator, a common formula, capable of infinite variations by slight alterations. His theory of evolution was more ideal than real, but it helped to pave the way for the full-blooded theory of descent with modification.

<sup>1</sup> 1875, p. 113.

<sup>2</sup> 1925, p. 5.

(b) *James Cowles Prichard* (1786-1848)

Professor Poulton<sup>1</sup> tells us how his friend Professor Meldola drew his attention to the second volume of *Researches into the Physical History of Mankind* by James Cowles Prichard and published in 1826. Of this book he says that it "anticipated in the clearest manner the arguments which have been recently advanced by Professor Weismann in favour of the non-transmission of acquired characters".<sup>2</sup> Poulton's paper in *Science Progress* is directed to an examination of the book from this point of view, and there is no doubt but that from the passages and descriptions given that Prichard did anticipate Weismann, and also Darwin to a limited extent. In a letter to Hooker, Darwin mentions Prichard in a statement from which it is difficult to tell whether he regards the latter as believing in the mutability or in the immutability of species.<sup>3</sup> On the other hand, Francis Darwin and A. C. Seward discuss Poulton's views regarding Prichard's belief in transformism. They acknowledge that Prichard was in advance of the times regarding the non-transmission of acquired characters, but, on the subject of evolution, they consider that Poulton has "unintentionally exaggerated the degree to which Prichard believed in evolution".<sup>4</sup> They quote many passages to show that this early writer contradicted himself in many places. In fact, then, this writer furnishes us with another example of those in whose minds the idea of evolution was beginning to take root. At this time there was an air of doubt floating over the mountain represented by the word "species", as indeed befits a period of formulation. Prichard's contradictions, like those of Buffon earlier, and like von Baer's queries, are then but characteristic indications of the trend of thought during these times.

However, as Prichard did anticipate Weismann to some extent we will give a short account of his views obtained from Poulton's paper and from *More Letters of Charles Darwin*.<sup>5</sup> Prichard was a medical man noted especially for his writings on anthropological and ethnological matters. Poulton tells us that he considered domesticated animals and plants had been produced by means of selection by man; and that he believed in transformism and

<sup>1</sup> 1897.<sup>2</sup> 1897, p. 278.<sup>3</sup> *Life and Letters*, 1888, Vol. 2, p. 29.<sup>4</sup> *More Letters of Charles Darwin*, Vol. 1, 1903, pp. 42-46.<sup>5</sup> Unfortunately I have been unable to get a copy of Prichard's book.

recognised the effect of natural selection. "The most important anticipation is, however, the masterly discussion on the transmission of acquired characters, a discussion in which the distinction between acquired and inherent or congenital characters is clearly drawn".<sup>1</sup> The two chief paragraphs referring to acquired characters are quoted below:<sup>2</sup> "It appears to be a general fact, that all connate varieties of structure, or peculiarities which are congenital, or which form a part of the natural constitution impressed on an individual from his birth, or rather from the commencement of his organization, whether they happen to descend to him from a long inheritance, or to spring up for the first time in his own person—for this is perhaps altogether indifferent—are apt to re-appear in his offspring. It may be said, in other words, that the organization of the offspring is always modelled according to the type of the original structure of the parent." "On the other hand, changes produced by external causes in the appearance or constitution of the individual are temporary, and, in general, acquired characters are transient; they terminate with the individual, and have no influence on the progeny."<sup>3</sup>

After giving examples to support these statements, Prichard points out that any varieties produced in a race have their beginning in the original structure of some particular egg or germ and not in any change induced by external causes. He then passes on to consider how domestic races have arisen, and he concludes, like Darwin, that cultivation of either animal or plant does not account for it, but what has happened is that man has artificially selected those individuals which possessed the characters desired in the highest degree. In nature he considered that the climate was the factor most influencing the production of varieties on organisms. He supposes that organisms have been placed in particular places so that their structure is adapted to particular environments. "But," he continues, "why is it to be supposed that the influence of this law of adaptation has stopped there? Is it not probable that the varieties which spring up within the limits of particular species are further adaptations of structure to the circumstances under which the tribe is destined to exist. Varieties branch out

<sup>1</sup> Poulton, 1897, p. 279.

<sup>2</sup> Poulton, 1897, p. 283.

<sup>3</sup> It may be pointed out here that the sentence in the first quotation beginning "It may be said . . ." could possibly be given as an example of Prichard's views regarding the immutability of species.

from a common form of a species, just as the forms of species deviate from the common type of a genus. Why should one class of phenomenon be without end or utility, a mere effect of contingency or chance, more than the other? There are indeed many instances in which we can perceive an advantage in the varieties of form, and an adaptation of particular breeds to external circumstances."

Later on he seems to have recognised that individuals, families, even colonies, perish from environments to which they are not adapted. It is here that Poulton considers that Prichard anticipated Darwin's idea of natural selection. But he did not pursue the matter beyond the mere recognition that a force (such as that of natural selection) operates in nature.

On the other hand Francis Darwin and Seward bring forward passages in Prichard's book showing that he believed in the immutability of species. Some of these are as follows:—"The meaning attached to the term species, in natural history, is very simple and obvious. It includes only one circumstance—namely, an original distinctness and constant transmission of any character. A race of animals, or plants, marked by any peculiarities of structure which have always been constant and undeviating constitutes a species."<sup>1</sup> And again: "Even those physiologists who contend for what is termed the indefinite nature of species admit that they have limits at present and under ordinary circumstances. Whatever diversities take place happen without breaking in upon the characteristic type of the species. This is transmitted from generation to generation: goats produce goats, and sheep, sheep."<sup>2</sup>

Although these two passages are put forward as showing that Prichard regarded species as immutable, they need not be taken as evidence that he did not recognise some kind of evolution of species. The last paragraph could stand equally as well today as it did then, depending on the meaning we give to the word *species*. Goats still produce goats and we cannot visualise them producing anything else. In evolutionary literature it is all too evident that there are as many variations of meaning of the word (according to the need or argument of the writer at the time) as there are varieties in polymorphic species. Prichard may have believed that species (in the sense of a 'common form') were immutable, and yet also believed that individuals could change and vary around that common form as round a mean. The fol-

<sup>1</sup> Darwin and Seward, 1903, p. 43.

<sup>2</sup> *ibid.*, p. 45.

lowing passage indicates this and also shows quite definitely that the idea of species change at this time was becoming a matter of 'conjecture' for naturalists. He writes: "There must, indeed, be some principle on which the phenomena of resemblance, as well as those of diversity, may be explained; and the reference of several forms to a common type seems calculated to suggest the idea of some original affinity; but, as this is merely a conjecture, it must be kept out of sight when our inquiries respects matters of fact only."<sup>1</sup>

Further detailed analysis of Prichard's works might yet show that his contradictions are apparent only, and that really he had grasped the idea of evolution quite firmly. He is then as much a forerunner of Darwin as any of those who believed in 'affinity' or 'unity of type,' or 'perfection', etc. But he differs from his successors in that he did not limit the meaning of the word 'species' to some small category within which evolutionary change is obvious. We can say, therefore, that he believed in 'microevolution' but was not quite certain about 'macroevolution'. He did not needlessly apply the doctrine of uniformity to matters of conjecture only. Thus he is typical of the advanced biological thinker of his day, and it is because of this that we have included him in our account of the naturalists of this period.

### 3. BARON CUVIER (1769-1832)

It is necessary now to introduce the most accomplished zoologist of the times. As a favourite of Napoleon and as head of the *Jardin de Plantes* in Paris "the illustrious Cuvier" exercised an immense and unparalleled authority over the contemporary biological world up to about 1858. In his introduction to his translation of the Frenchman Milne Edwards' *A Manual of Zoology* R. Knox describes Cuvier as a man "destined to revolutionize all zoological science, viewed under every possible aspect".<sup>2</sup> But he was by no means an evolutionist, and he opposed the rise of the new, as yet little understood, cosmogony with all his ability. By his controversy with Geoffrey St. Hilaire he retarded speculations upon the evolution idea. Osborn considers that whenever Cuvier entered the realms of speculation he became "exceptionally un-

<sup>1</sup> Darwin and Seward, 1903, p. 44.

<sup>2</sup> 1856, p. xix.

sound", while Sedgwick and Tyler<sup>1</sup> describe him as clinging "tenaciously to the theory of Special Creation". Contrast these rather dismal pronouncements about a genius with that of Merz who wrote: "Cuvier had also a true historical sense, which enabled him to trace the connection of science with political history, with literature, with the fine and useful arts".<sup>2</sup> Cuvier had no need to cling tenaciously to any theory because all his ideas rested on the sure foundation of conviction. His contribution to science made him pre-eminent among the scientific men of his century. While his theory of special creation of the major forms of animals harmonised well with his geological views on catastrophism as being the only reasonable explanation of the great changes which have occurred in the strata of the earth. The one view was the logical outcome of the other. "*On est obligé d'admettre certaines formes, qui se sont perpétuées depuis l'origine des choses, sans excéder ces limites; et tous les êtres appartenants à l'une de ces formes constituent ce que l'on appelle une espèce*".<sup>3</sup>

Daudin points out that, contrary to a widespread opinion among many evolutionists, Cuvier, more even than Lamarck, prepared the way for the overthrow of the old scientific dogmas regarding the nature of the affinities between organisms. Daudin wrote: "In the long run, in denouncing the edifying arbitrariness of 'serial' representation of the living world, in recognising the very unequal degree of connections between zoological types, and finally in admitting that the number and distribution of species according to their characteristics can be overturned in exceptional, but decisive, cases by physical events, Cuvier has more than anybody set out the first half of the conditions necessary for Darwin. Thanks to him, it has been established that the simple play of circumstances can at least destroy bit by bit the economy of nature".<sup>4</sup>

Cuvier, in fact, did much to establish the science of palæontology as the study of the succession of animal forms in the rocks of the earth. Although there had been many before him, some like John Hunter, who had examined an imposing array of fossils, none had been led to say that species of animals had ever become extinct, or that new ones had appeared. As Richard Owen<sup>5</sup> says: "The foundations of palæontology cannot be said to have been laid before

<sup>1</sup> 1929, p. 373.

<sup>2</sup> 1896, Vol. 1, p. 138.

<sup>3</sup> 1816, Vol. 1, p. 20.

<sup>4</sup> 1926, Vol. 2, p. 256.

<sup>5</sup> 1866, Vol. 1, 312.

his (i.e., Cuvier's) time". He was among the first to compare the structure of fossil and present existing animals, and thus he showed that past existing animals had to be taken into account in the study of living things. By his detailed studies of living and extinct animals he was led to realise the importance of the principle of correlation of parts of animals; he carried this principle to its extreme limits. Cuvier refused to believe that the record of the rocks indicated a transformism of species; his poor attempts at speculation (according to Osborn) are quite easy to understand when we see how successful he was in his application of these principles of correlation. For, from a tiny piece of leg bone Cuvier made a reconstruction of a giant bird which later proved to be correct. Cuvier did not need any concept of genetic evolution: he was highly successful without it, and he could arrive at an excellent natural classification by his application of his own methods. The following sentence sums up his views in this respect and it certainly shows that he had a thorough grasp of both philosophical and scientific principles: "The pretended scale of beings is but an erroneous application to the whole creature of those partial observations, which are only true when confined to the limits within which they were made".

Throughout his work Cuvier was attempting to arrive at general biological laws; and yet he discarded what seems to us to be the most important generalisation and unifying principle of them all. Perhaps he was prevented from this by his very definition of a species as "the re-union of individuals descended one from the other, or from common parents, or from such as resemble them as strongly as they resemble each other".<sup>1</sup> He knew many species had become extinct and whenever a new one was found in a stratum of the rocks, he thought that it had been specially created during a period of time when that stratum was laid down.

Cuvier's method of study was analytic and was based on the internal and external structure of animals. Thus he was able to give to the zoological world his great contribution *Le Règne Animal, distribue d'après son organisation* published in 1816, which opened up a new era in comparative anatomy. In this book he rejected Lamarck's simple dichotomy into vertebrates and invertebrates, and established four large groups as follows:—

- |                             |  |
|-----------------------------|--|
| (a) the <i>Vertebrata</i> , | (b) the <i>Mollusca</i> ,                      |
| (c) the <i>Articulata</i> , | (d) the <i>Radiata</i> , or remaining animals. |

<sup>1</sup> *Le Règne Animal*, 1816, Intro., p. 8.

Starting with these groups, he worked out a complete and logical system of classification of probably all the animals then known. The mere list of orders, families and genera occupies twelve pages of H. McMurtie's translation.<sup>1</sup> There are upwards of 950 genera and sub-genera. In volume one of an English translation we read in the Memoir of Cuvier:<sup>2</sup> "Whilst Aristotle exhibited wonderful judgment in his arrangements still he had no true notion of the laws which regulate species; he was confounded altogether by the limits of the variations of species, and here it is that the second Aristotle has been able triumphantly to succeed. Cuvier studied ardently and incessantly the nature of the conditions that allow of the development of individuals or species in the form in which they appear, and the results of his original and wonderful labours have cast a light over the mysteries of living nature, such as discloses them in a condition in which they are most calculated for our comprehension. Cuvier in traversing the relics of the ancient world, and comparing them with the structures which compose the breathing beings of this, discovered the talisman which opened every locked treasure to his hand, in the simple law that every part of any animal, and in some, the very smallest, constitutes a certain index of the character in all respects of the rest. The successful application of this law is one of the greatest triumphs of the genius of Cuvier." A corollary of this law is that each part of an animal is expressly made to fit in with all the other parts. It was probable that this corollary formed the barrier between Cuvier and St. Hilaire who believed in homologies between structures. Like Goethe, then, Cuvier recognised a certain unity of plan among animal types which could be applied to the working out of schemes of classification. In 1798, indeed, before the publication of his *Animal Kingdom*, he gave us the following axioms: "*Deux espèces quelconques d'êtres organisés ont nécessairement quelques points d'organisation par lesquels elles se ressemblent. Ces points d'organisation sont ce qu'on nomme leurs 'rapports naturels'. Plus ils sont nombreux, plus ces 'rapports' sont 'grands'.*"<sup>3</sup>

Incidentally Cuvier includes man in the *Mammalia*, but puts him in a separate order, the *Bimana*, as distinct from the *Quadrumana* which includes the monkeys, apes, etc. In the order *Bimana* there is only one genus.

<sup>1</sup> 1834.

<sup>2</sup> 1834, p. xiii.

<sup>3</sup> 1798, p. 15.



In the preface to the *Règne Animal*<sup>1</sup> we read "I have ever kept in view as the object of my labours, the resolution of the science into general laws and into propositions of the simplest expression". Cuvier realised that this could only be accomplished by arranging the animals into natural groups, such as classes, orders and genera. In these groups he placed only those types which resembled each other in internal and external structure. The members of each group then gave some indication of the general and particular affinities uniting them. Thus animals had to be arranged in a system of classification which would allow one to discover any natural organisational law referring to each group. Previous arrangements had not been able to do this. Cuvier was not so much concerned with size and colour, or other such differences, or with the materials of which they were composed, as with the characters both internal and external which enabled one to grasp the "essence of each animal". The *form* of a living body is much more essential to it than its *matter*. Thus Cuvier seemed to have reckoned that the more the essences of animals resembled each other, or conformed to a common plan, then the closer their natural affinity. Affinity here does not necessarily imply genetic or blood relationship for he is very careful to point out that he does not desire to class animals into a single line with the least perfect at the bottom and the most perfect at the top. In fact he calls the expression "the most perfect" a *vague expression*. It means simply the most completely organised. Cuvier had left the Aristotelian idea behind.

#### 4. CUVIER'S CONTEMPORARIES

Geoffrey St. Hilaire gave definite expression to Goethe's rather nebulous ideas of analogies. This colleague of Cuvier's for more than thirty years, laboured to try and elucidate the relations between organisms which he saw in their analogies, while Cuvier worked to describe things and fit them into a natural classification. St. Hilaire's researches led him to recognise a fundamental unity among living things which he called the *unity of organic composition*. Merz<sup>2</sup> reminds us that in this he only gives more precise expression to a truth which Aristotle and Buffon both proclaimed, i.e. that living things exhibit "unity of plan combined with variety of composition". Cuvier emphasised and studied the latter; his colleague the former. For an intimate knowledge and description

<sup>1</sup> 1st Ed., p. xvii.

<sup>2</sup> 1903, Vol. 2, p. 255.

of natural objects the work of distinguishing is all important; for a comprehension of nature the connection of things, the unity of plan, and the relationships of things will always be the more important. Merz finishes by reminding us that Cuvier's task was purely scientific, while St. Hilaire's was more philosophical. St. Hilaire was more interested in the internal structure of animals and the functions of their parts than in morphology.

A real scientific, as distinct from philosophical, theory of evolution could scarcely emerge until the various branches of biology such as anatomy, embryology, geographical distribution and also palæontology, had developed sufficiently to allow generalisations to be made. The work of the classifiers in the eighteenth century paved the way for this further development, but it was not until the nineteenth century that laws and principles were established. We have already seen that Cuvier put comparative anatomy on a solid basis, while at the same time he developed palæontology sufficiently to shatter some of the ideas of the special creationists—the majority opinion of the times. His discovery that some species had become extinct introduced a real difficulty into the orthodox view. For then it became necessary to postulate a very large number of distinct and separate creations. It also raised the question: why did some species cease to exist? Cuvier himself was, however, a firm believer in special creationism. T. H. Huxley tells us somewhere that he wavered in this opinion but he never seems to have attempted to retract it. And no wonder; it would have meant recasting all of his immense store of factual knowledge. His belief in the fixity of species was not, as some writers have suggested,<sup>1</sup> due to his antagonism to the *Naturphilosophie*.

Thus, while Cuvier and others were busy showing that there had been a succession in time of forms as depicted in the various strata of the earth's crust, G. St. Hilaire, also an anatomist, attacked the problems from a different angle. St. Hilaire was, as his son Isidore St. Hilaire shows, a disciple of Buffon, but he also came under the influence of Lamarck's *Zoological Philosophy* and, in fact, he developed many of Lamarck's principles. According to Osborn<sup>2</sup> he took up the study of evolution at the point where Lamarck left off. His view of the concept was positive and he definitely entertained the genetic principle of descent by modifi-

<sup>1</sup> T. H. Huxley, *Life of Owen*, Vol. 2, p. 295.

<sup>2</sup> 1924, p. 198.

cation of more complex species from simpler ones. He was a Lamarckian, but, while admitting the action of the environment in shaping the destinies of species, he denied that the fundamental activities of organisms had any effect; in other words, the habits of animals could not produce an inherited morphological change. St. Hilaire did not overlook the occurrence of saltations (or mutations) as a possible method whereby new forms arise. While he was at the height of his speculations on transformism the famous debate, which the old man Goethe thought of far greater importance than the French Revolution of 1830, ensued. In this debate, before a large scientific audience, Cuvier scored a decided tactical victory and managed to oust St. Hilaire from his position on every one of his points. The immediate result in France, where the debate occurred, was that the question of evolution dropped out of the popular scientific horizon. Geoffrey St. Hilaire, however, had set a seed which could never again be refused germinating room. Eckerman relates in his "Conversation with Goethe" that Goethe, referring to this debate, said: "What is best is that the synthetic treatment, introduced by Geoffrey in France, cannot go back again".<sup>1</sup> A detailed account of this debate has been given by Ducratay de Blainville.<sup>2</sup>

### 5. RICHARD OWEN

G. St. Hilaire has been called the "father of homology". To a certain extent this is true, for in several works, chiefly that on the *Bones of the Skull in Birds*,<sup>3</sup> he set out to find homologous structures. Other workers in this field before and contemporary with him were Cuvier, Oken, Mecken and Agassiz. Oken<sup>4</sup> had endeavoured to trace the general homology of the bones of the skull with the vertebrae of the vertebral column. Still, however, there was a good deal of confusion as to the precise meaning of the word "homology" as contrasted with "analogy" in natural science. As Owen points out,<sup>5</sup> the term analogy was sometimes used to express the idea of the term homology.

Thus the real exponent of the principle of homology was not St. Hilaire but the English comparative anatomist Richard Owen,

<sup>1</sup> See Merz, 1903, Vol. 2, pp. 253-4.

<sup>2</sup> 1890, pp. 357-8.

<sup>3</sup> 1847.

<sup>4</sup> 1807.

<sup>5</sup> 1846, p. 174.

who follows on from Cuvier across the nineteenth century till after the publication of the *Origin of Species* and the death of its author. Owen gave precise meaning to the word "homology" as used in natural history, and he brought it into general use. In the glossary to his *Lectures on Invertebrate Animals*<sup>1</sup> he defines an *analogue* as a part or organ in one animal which has the same function as another part or organ in a different animal; and *homologue* he defines as the same organ in different animals under every variety of form and function. The one is relative to the function of a part independent of its morphology, while the other is relative to the morphology of a part independent of its particular function (which may in fact vary in different animals). Later<sup>2</sup> he expands this definition in a long paper in which he recognises three kinds of homology, viz. general, special and serial homology.

Owen, unlike Cuvier, allowed that some degree of natural transformation of species had taken place; and yet he was not a Darwinian evolutionist. By his clarification of the meaning of homology, he did much to simplify the task of comparative anatomists with an evolutionary bias. We must remember that the evolution theory obtains strong evidence from anatomy. Indeed, take away this anatomical evidence and it would be very difficult to establish a sound theory of evolution in spite of, perhaps because of, the geological evidence. While homology and analogy were not clearly defined it was impossible for anatomy to become a line of evidence supporting the theory of evolution in its modern sense. By applying the principle of homology, as taught by Owen, to comparative anatomy, biologists have been able to discover the deeper relationships between animals and parts of animals. This could never have been done with the use of morphology alone. Later this principle was extended to include the developmental stages in its scope, and so the way was paved for the recognition of the genetic (or blood relationship) point of view.

About this time William Mackey first clearly discerned the difference between those similarities of animal structure that indicate an *affinity* and those that indicate an *analogy*. Affinity refers to similarity of complete structure; the closer animals resemble each other the closer is the affinity between them. Owen<sup>3</sup> is careful to point out that affinity has a completely different meaning

<sup>1</sup> 1843.

<sup>2</sup> 1846, pp. 169-340.

<sup>3</sup> 1858, p. lxvii.

to homology. He says, "Animals, however, intimately 'affined', are never the same in the sense which homologous parts are so esteemed: they could never be called by the same name, in the way or sense in which a bone, for example, of the forelimb is called 'humerus' in the goat-sucker, swallow and bat". Hence even as late as 1858 in that century of active research the word affinity receives its first precise definition and in that definition there is no hint that it indicates a genetic relationship among the things 'affined'. No matter how similar two species are in their outward structural plan they remain distinct species with no blood relationship. Homologous parts in a common group of animals indicate, according to Owen, a deeper relationship than mere affinity, for it bears out the essential unity of plan and shows the relationship of the types to the archetype of them all.

This notion of a basic archetype underlying the plan of the structure of animals constantly recurs in the works of Owen. The skeletal archetype is manifestly segmented. This principle of segmentation is common to animal types and becomes more and more emphasised as we descend the scale of animal creatures. This form of development appears to be the result of 'vital properties', or to be due to the operation of 'vital principles' (corresponding to Plato's *ideai*). To these Owen adds a polarizing force which acts against the vital force and is responsible for the unity of organisation of living bodies. "The Platonic idea, or specific organizing principle or force, would seem to be in antagonism with the general polarizing force, and to subdue and mould it in subservience to the exigencies of the resulting specific form".<sup>1</sup> He repeated this idea of two contending forces later in his *Principes d'Ostéologie comparée*<sup>2</sup> and he probably made it one of the bases of his well known work on comparative anatomy and physiology. In this book,<sup>3</sup> however, he definitely connected the "principles of development through polar relations" with the attainment of a final aim as a result of a pre-ordained purpose.

Owen further extends this unity of plan idea to man whom he puts as a separate species in a separate order. In spite of the resemblances of man to the apes he finds that the real indications of their unity to the type are shown by the constancy of their dental and other osteological characters which are peculiar to

<sup>1</sup> 1846, p. 339.

<sup>2</sup> 1855, p. 366.

<sup>3</sup> 1866, Vol. 1, Preface, p. x.

him. Man has "no nearer physical relations with the brute kind than those which arose out of the characters that link together the great groups of placental *Mammalia*, called *Unguiculata*".<sup>1</sup> It is interesting to note that with the discovery and use of homologies and analogies in natural history arose the dependent idea of an archetype, or ideal organism, which embodies potentially all the other organisms. Ray Lankester<sup>2</sup> pointed out that the abstraction of an *ideal type* was necessary in order to settle which organs were homologous (i.e., which were the same despite differences of form or function). The alternative was evolution by descent.

Palæontological series revealed to Owen that, as we descend the earth's strata, the organisation of species tends to become less specialised and more generalised. Indeed, extensive research in palæontology and anatomy led him to modify his original views of the immutability of species. "Accordingly", he says, "these results of extensive, patient, and unbiassed inductive research—or, if there were a bias, it was towards Cuvier—swayed with me in rejecting the principle of direct or miraculous creation, and in recognising a 'natural law' or secondary cause as operative in the production of species 'in orderly succession and progression'".<sup>3</sup> This was, of course, written after the publication of the *Origin of Species*.

Owen, then, came to believe in descent with modification, i.e., in evolution as we understand the term today. It was the fossil series, especially that of the horse, which led him to this belief. As a pupil, and to a great extent a follower, of Cuvier, he believed in his teacher's conclusions. It was obvious to Owen, as to his teacher, that if geology were to be of any use in deciding for or against this theory of descent, then intermediate stages in the process of change from one species, or type, into another were absolutely necessary. While evidence of these stages was lacking Owen rejected the new idea. When evidence of several such stages was found he accepted the theory of descent as a reasonable way of interpreting the facts, and one which was more scientifically justifiable than the assumption of the occurrence of special creations. As he says, 'If the alternative—species by miracle or by law?—be applied to *Palaeotherium*, *Palaeoplotherium*, *Anchitherium*, *Hipparion Equus*, I accept the latter, without misgiving, and recognise such law as continuously operative throughout tertiary time".<sup>4</sup>

<sup>1</sup> 1855, p. 112.

<sup>2</sup> 1870, 4th Ser., Vol. 6, p. 34.

<sup>3</sup> 1866, Vol. 3, p. 789.

<sup>4</sup> 1846, p. 193.

While recognising the possibility of an evolution of species, Owen does not extend this particular case (i.e. of the horse series) to cover the whole animal kingdom, or even to cover the condition of the horse ancestors before the tertiary era. Incidentally Owen does not call this sort of thing *evolution*—he seems to prefer the term *transmutation*. He clings to the old meaning of the former word, that is, the gradual development of an animal from the embryo to adulthood. It is sometimes contended that Owen was an anti-evolutionist, but this is certainly not so; he was, however, an opponent of the special Darwinian theory of the cause of evolution, which is another matter altogether. The change over of the pupil of Cuvier to become an upholder of the fashionable evolution theory was certainly sudden and complete, when, only in 1855, he could write: "Of the nature of the creative acts by which successive races of animals were called into being we are ignorant".<sup>1</sup> The exact way in which species change is determined by the Creator and further, according to Owen, seems to follow the original unity of type plan. As regards the secondary cause of the change in the *Equus* type, Owen discards a Lamarckian explanation, but he just as emphatically rejects a Darwinian one. He excludes natural selection by going back to first philosophical principles.

His criticism here still stands today, although it is to a very large extent ignored (this being the trend of the times). "Assuming, then that *Palaeotherium* did ultimately become *Equus*, I gain no conception of the operation of the effective force by personifying as "Nature" the aggregate of beings which comprise the universe, or the laws which govern these things, by giving to my personification an attribute which can properly be predicated only of intelligence, and by saying 'Nature has selected the mid-hoof and rejected the others'."<sup>2</sup> Owen recognises that there is a struggle for existence among species which leads to the extinction of some of them. But extinction is not creation. If, in some cases, natural selection does seem to explain the survival of certain higher types of animal, it should also be applicable to the lower creation. Owen then proceeds to show how the theory cannot be applied to the evolution of the life-forms in an atoll, or similar coral bound lagoon. The Lamarckian explanation fails to act as a sufficient secondary cause, too, for such things as holothurians can scarcely be said to possess volitional powers. The Lamarckian theory has only a limited

<sup>1</sup> 1855, p. 112.

<sup>2</sup> 1866, p. 794, and footnote pp. 798-800.

applicability. Thus, after having considered the then current explanations of the ways by which species could change, Owen is driven to reject them as insufficient. An explanation, however, is still necessary. A secondary cause has been shown to be operating in the evolution of species. So Owen concludes that "an innate tendency to deviate from parental type, operating through periods of adequate duration, to be the most probable nature, or way of operation, of the secondary law, whereby species have been derived one from the other."<sup>1</sup> This is Owen's *Derivative Hypothesis*, and it fits in with his general basic scheme whereby there is a unity of plan in animal types in which changes can occur in a pre-ordained direction under the fiat of an Intelligent Directing Power. This, then, closely resembles what we would now call orthogenesis, the causal theory of evolution beloved of the palaeontologists.

## 6. PALAEOLOGY

During this period the important science of palaeontology came into being. Previous to the eighteenth century the age of the earth was estimated at about six thousand years in conformity with calculations based upon the Bible. Thus it is easy to understand how everyone believed in the immutability of species. Although fossils had been known for very many years previous to this century (Aristotle knew of some of them), few people seem to have realised their full significance. As William W. Watts says,<sup>2</sup> they were at first "thought to be merely *lusus naturæ*". But we can pass over these farcical suggestions that the fossils were merely put in the rocks by the Creator to confound the men of science, or the excusable idea of Fallopius that they arose by some process of fermentation. Since Bishop Nicolaus Stensen's day fossils have been recognised to be of organic origin. From the beginning of the eighteenth century onwards an ever increasing number of fossils was found until by the time Cuvier began to take an interest in the subject very many different types were known and had been described. Cuvier's own researches led him to conclude (1) that there is a distribution in time of organisms in the strata of the earth, and (2) that some of the fossils were the remains of animals which had become extinct. As we have already indicated, Cuvier is to be regarded as the founder of palaeontology. To explain the fact that

<sup>1</sup> 1866, p. 807.

<sup>2</sup> In *Evolution in the Light of Modern Knowledge*, 1932, sect. Geology, p. 60.



some species had become extinct and others appeared suddenly he was forced to bring in the theory of catastrophism. In 1817 William Smith (1769-1839) published his *Stratigraphical System of Organised Fossils* in which he showed that fossils occurred chiefly in stratified rocks. Smith's book also sounded the death knell of the catastrophic theory by showing that some fossils of a series may be found in the stratum below its chief one, and others of the same series in that above; while some were found in all three. This fact was most difficult to reconcile with the catastrophic theory. Finally in 1830, Sir Charles Lyell (1797-1875) published his standard textbook *The Principles of Geology* in which he demonstrated how rocks are even now being formed by sedimentation of debris carried down from higher regions to lower regions by rivers, and also by disintegration of existing rocks by weathering processes. Lyell also considered that the earth was, not six thousand years old, but millions of years and during all this time small changes had been constantly occurring.

Lyell's work was essentially uniformitarian in its teaching, for the great feature of his book is that in it he showed that the earth has had a continuous and progressive history. This implies that the organic contents of the rocks (i.e., the fossils) also have had a continuous history. Indeed Lyell had read Lamarck's *Zoologie* with favour, but without accepting the theory, and he later became a convert to Darwin's views; Darwin was immensely gratified. Lyell in fact claims that his book prepared the way for Darwin before the appearance of Chambers' *Vestiges of the Natural History of Creation*. In a letter to Haeckel written in 1868<sup>1</sup> he says: "But while I taught that as often as certain forms of animals and plants disappeared for reasons quite intelligible to us, others took their place by virtue of a causation which was beyond our comprehension; it remained for Darwin to accumulate proof that there is no break between the incoming and the outgoing species, that they are the work of evolution and not of special creation. . . . I had certainly prepared the way in this country, in six editions of my work before the 'Vestiges of Creation' appeared in 1862, for the reception of Darwin's gradual and insensible evolution of species".

In the nineteenth century then geology and palæontology became recognised sciences. Gradually animal series of fossils were unearthed; in many cases reconstructions of organisms were built up from a few bones. As far as palæontological research

<sup>1</sup> Lyell : *Life and Letters*, Letter to Haeckel, Vol. 2, p. 426, 1868.

was concerned, the workers during this period were Cuvier, Owen between 1837 to 1887, Louis Agassiz on fossil fishes, de Blainville, von Meyers and many others. As time passed by it became difficult to fit all fossils into existing groups or organisms, and so new intermediate groups arose in the classifications. Palæontology revealed a succession of organisms in the earth's strata and also showed that as we ascend from the older to the younger layers of the earth there is an increase in the similarity of the fossils to the existing fauna. In spite of this, however, we find Agassiz (1807-73), as late as 1851, stoutly denying that this implies any genetic succession of species. He<sup>1</sup> says: "But this connection is not the consequence of a direct lineage between the faunas of different ages. There is nothing like parental descent among them. . . . The link by which they are connected is of a higher and immaterial nature; and their connection is to be sought in the view of the Creator himself whose aim in forming the earth, in allowing it to undergo successive changes which geology has pointed out, and in creating successively all the different types of animals which have passed away, was to introduce man upon the surface of our globe. Man is the end towards which all the animal creation has tended, from the first appearance of the first Palæozoic fishes."

Nevertheless, it is fairly clear that these discoveries in palæontology succeeded in laying a foundation for the future enlargement in a biological sense of the theory of evolution. We can remember here that Lamarck's contributions in this direction were turned down—he attacked the problem from the purely biological side, whereas in Darwin's *Origin of Species* one of the chief, if not the most important, line of evidence for the reality of organic evolution was that based on palæontology. This science, in fact, serves as the historical museum of the subject which is itself the history of organic beings. This point was realised by men like T. H. Huxley<sup>2</sup> who indeed declared in 1888 that a "discerning eye might have seen that some form or other of the doctrine of transmutation was inevitable, from the time when the truth enunciated by William Smith, that successive strata are characterised by different kinds of fossil remains, became a firmly established law of nature". Huxley then goes on to quote Whewell<sup>3</sup> who, in 1847, wrote to the effect

<sup>1</sup> 1851, p. 238.

<sup>2</sup> *Life and Letters of Charles Darwin*, ed. by F. Darwin, 1887, p. 193.

<sup>3</sup> W. Whewell, *History of the Inductive Science*, 2nd Ed., 1847, Vol. 3, pp. 624-625.

that the study of geology reveals that we must either accept the theory of transmutation of species or the creation of species by miraculous acts.

## 7. THE CELL THEORY

### (a) *The Groundwork of the Theory*

From the beginning of the nineteenth century the foundations of a new science were gradually laid down. This was the science of *cytology*. The recognition of the important role played by the cell in the life of an organism emerged from the observational data which were now steadily accumulating. Previous to this century biologists had tended to examine the macroscopic parts of animals rather than their inner structure; later their attention was turned to the microscopic parts of animals. In fact there is a progression of investigation from organs to cells from about the time of Harvey.

In 1651 in his *De Generatione Animalium* William Harvey (1578-1657), the discoverer of the circulation of the blood, described the growth of an embryo. He even grasped the idea of epigenesis, or progressive development of tissues. From Harvey it is a far cry to Aristotle who had also grasped this principle and who was actually the first to study the development of the chick embryo. Malpighi (1628-94) examined glands and other tissues and did much to lay the foundations of modern embryology. In 1665 Robert Hooke introduced the word *cell* into biology to describe the compartments into which the bodies of higher plants could be resolved. Rather later A. von Leeuwenhoek (1632-1723) discovered what we now call spermatozoa, blood corpuscles, and even bacteria. Much later still Casper Frederick Wolff (1733-1794) studied the growth and differentiation of cells through a microscope, and he seems to have had a thorough grasp of their structure, but he did not realise their significance. In his *Theorie Generationis* of 1759 he was really the first to demonstrate that the fertilised egg did not contain an homunculus. He thus, at one fell swoop, shattered the quaint, but widely held, views of the animalculists who believed that either the egg of the sperm contained a miniature, but completely formed, embryo, which had only to unfold itself, or 'evolve', in the mother's uterus.

In 1827 Karl Ernst von Baer (1793-1876) discovered the human egg and he described it as differing in no essential respects from the

eggs of other animals. Then in 1828 he published the first important book on comparative embryology, announcing that mammals and man reproduce by means of eggs just as do the lower animals. Thus von Baer has been hailed as the founder of modern embryology.<sup>1</sup> The establishment of embryology was a stimulus to further research into cells and their manner of differentiation; but now the point of view changed. Previously they had been looked at as parts of tissues, now they began to be seriously studied as individual wholes. Eventually the cell theory itself was formulated.

To begin with, in 1831, Robert Brown found that the nucleus was a regularly occurring constituent structure of all plant cells. The cell theory then grew out of the earlier work of these investigators, and from the work of Johann Purkinje (1787-1869) who, in 1835, compared the cells of plants with those of animals, and also from the work of Felix Dujardin (1801-62) who, about the same time, was able to distinguish unicellular organisms from multicellular ones. Dujardin was also the first to recognise that living cells always contained a certain substance with definite properties. Purkinje, in 1839, gave this substance the name "protoplasm". He compared it to the granular substances of the cambium in plants. Dujardin had used the term "sarcode" to designate the contents of cells of the *Protista*. The word protoplasm was afterwards used quite independently by von Mohl in 1846 for the liquid contents of plant cells. Earlier, in 1805, Oken, whom we have already mentioned, recognised the contents of cells to be a distinctive substance and he gave it the name of *Urschleim*. He contended also that animals were made up of masses of numerous vesicles or cells and were just, in fact, masses of *Infusoria* joined together. M. Schultze (1825-1874) found that the protoplasm of both plant and animal cells is essentially of the same nature, and is usually nucleated. In 1863 he recognised it as the "physical basis of life", a phrase which T. H. Huxley used later in 1868.

(b) *The Formulation of the Theory by Schleiden and Schwann*

By 1838, Schleiden (1804-1881) and Schwann (1810-1882) had first formulated their now famous cell theory. The former worked on plants and the latter on animals and, after collaboration, they enunciated the principle that as organisms are made up of cells,

<sup>1</sup> See Sedgwick and Tyler, 1929, p. 375, and Nordenskiöld, 1929, p. 363.

or cell products, each cell has a certain life of its own, and yet all the cells of a body are subject to the life of the whole organism. Schwann gave a full account of the theory in his *Mikroskopische Untersuchungen über die Uebereinstimmung in der Struktur und dem Wachstum der Thiere und Pflanzen* in 1839. The fundamental point of the theory is that, as Sharp points out,<sup>1</sup> all cells, no matter what their appearance, are morphologically equivalent, and as living units their action determines the development of the whole organism—"the cell is the primary agent of organisation". As Schwann says in the paper referred to above: "The development of the proposition that there exists one general principle for the formation of all organic productions as well as the conclusions which may be drawn from this proposition, may be comprised under the term *Cell Theory*".<sup>2</sup>

According to Wilson,<sup>3</sup> this cell theory of Schleiden and Schwann ranks in importance with the theory of evolution. "Every field of biological research has been illuminated by the cell theory. In respect to the range and diversity of the phenomena which it has brought under a single point of view it is surpassed by no other of the great generalisations of biology, and equalled only by the theory of organic evolution. By force of habit we still continue to speak of the cell 'theory' but it is a theory only in name."

From the time of its authors, the theory advanced from a vague conception to become the science of cytology under the able hands of men like Virchow, de Bary, Unger and Beales. Schleiden and Schwann had thought that the cells arose more or less *de novo* by some kind of free cell formation from a formless mass of substance. This idea of the appearance of the cells themselves was a stumbling block to any further real advance. The difficulty was only finally overcome when, in 1885, Virchow enunciated his famous aphorism '*omnis cellula e cellula*'.<sup>4</sup> The reality and universality of cell division was then fully recognised. Towards the end of the nineteenth century theoretical considerations began to enter into the discussions of cytologists under Weismann (who put forward the theory of the continuity of the germ plasm), Nägeli, Butschli, Hertwig and many others, until the final stage was reached with the rediscovery of Mendelism in 1900 by Tschermak, Correns and

<sup>1</sup> 1934, 3rd Ed., p. 429.

<sup>2</sup> Paper above, 1839, trans. in Sydenham Soc., 12, London, 1847.

<sup>3</sup> 1928, 3rd Ed., Intro., pp. 1-2.

<sup>4</sup> 1855, p. 23.

de Vries. Soon after, cytology became linked with genetics under the term *cytogenetics* when Sutton in 1903 showed that the behaviour of the chromosomes in cell division offered a cytological explanation of Mendelian phenomena.<sup>1</sup> Sutton then, along with Weismann, enabled biologists to bridge the gaps between cytology, genetics and the study of evolution. These three subjects are now so closely linked together that J. B. S. Haldane can write: "An attempt to study the evolution of living organisms without reference to cytology would be as futile as an account of stellar evolution which ignored spectroscopy."<sup>2</sup> It is cytogenetics which has given us our modern causal theory of evolution. This may eventually turn out to be a mixture of the Darwinian, Lamarckian and mutation theories.

<sup>1</sup> 1903, pp. 231-251.

<sup>2</sup> In Preface to C. D. Darlington's *Recent Advances in Cytology*, 2nd Ed., 1937.

## CHAPTER 5

### THE FORMULATIVE PERIOD CONTINUED :

#### (C) CHARLES DARWIN AND DARWINISM

##### I. INTRODUCTION

The years between 1859 and the end of the century mark the time during which the now historical concept of evolution took a firm hold on the scientific workers of the period. It spread from them far and wide into literature, language, history, chemistry and even into politics.

As we have followed the teachings from the earliest times of some of the outstanding workers in natural science, it has become evident that this science lacked a unifying principle upon which its laws could be built. In the early period the passion for classifying things reflected an almost subconscious feeling among the classifiers that their scheme should have some real substantial meaning, and not be purely arbitrary. Later, the Natural Philosophers, with or without a scientific background, introduced the idea of change into the purely biological world. But it was left to Kant in his *Critique of Judgment* to give the first precise definition of the relationship between species (now becoming regarded as mutable) as a direct blood connection. The idea of evolution was thus formulated and from this time onwards it gradually expanded until it became a recognised principle.

In fact it is true to say that the philosophers nursed the idea long before the biologists could legitimately adopt it. The poet Goethe, under the influence of Kant, affirmed an evolution of the expression of an archetype. Until, finally, the philosopher Spencer gave us his thoroughly worked out system of evolution in his *First Principles*, but the exposition of evolution which it contained had been published in separate parts, beginning in 1852, before the *Origin of Species* appeared in 1859. Spencer's evolution took in the whole of the cosmos, while Darwin's embraced only the organic world. According to Spencer : " Evolution is an integration of matter and concomitant dissipation of motion: during which the matter passes

from a relatively indefinite, incoherent homogeneity to a relatively definite, coherent heterogeneity; and during which the contained motion undergoes a parallel transformation.<sup>1</sup> This rather meaningless formula is meant to convey the principle that higher forms were produced from lower ones. Spencer's system of evolutionary philosophy soon became widely known and it probably did much to prepare the world for the publication of the *Origin of Species by Means of Natural Selection*, but it soon fell into disrepute, and now his writings are probably considered too boring to read.

Nevertheless, philosophizing apart, Spencer did much to bring the concept of evolution before the world in general. As Prof. Sir Edward Poulton<sup>2</sup> remarks: "But . . . we must never forget that believers in the doctrine of organic evolution owe an immeasurable debt to Herbert Spencer".

Darwin, during his travels in the *Beagle*, was impressed with the multiplicity of the natural objects he encountered. Then, and later, during the years after his voyages, he discerned a certain orderliness among species. The idea of evolution began to grow in his mind and he set himself the task of showing that it does occur. When he applied the idea of natural selection to his idea of evolution then the way by which nature produces new species seemed to him to be most clear and convincing. Thus the Darwinian theory of evolution came into being. Actually, Darwin's establishment, if not of the fact of evolution, then of its great probability, is really his greatest contribution to science. Too often this fact has been overlooked due, no doubt, to the more immediate appeal of natural selection, and to the over-emphasis which neo-Darwinians such as Weismann and Wallace placed on this operative factor to the exclusion of all else. By his masterly array of cumulative evidence from morphology, classification and the like, Darwin, more than any other previous scientist, established the theory of evolution as the great generalisation of contemporary biology. By direct appeal to numberless observations and without any hint of the invocation of mystical forces, Darwin succeeded widely where Lamarck had failed dismally.

Having established the theory of evolution on a firm basis, Darwin's next task was to give a causal explanation of the *way* in which species changed. Thus he had to find a force of universal application in biology. This force was found to be the irresistible natural selection: the force of Destruction, the "Creator".

<sup>1</sup> 1910, p. 321.

<sup>2</sup> 1937, p. 10.



## 2. CHARLES DARWIN AND "THE ORIGIN OF SPECIES"

It is now necessary to examine the theory of evolution known as "Darwinism", and here the examination will be chiefly confined to the theory as developed in the famous book *The Origin of Species by Means of Natural Selection*. We will see in a rapid review what were the chief tenets of the theory, while leaving the modern interpretation to a later chapter, when most of the examples will also be dealt with. In this account several general criticisms will be offered, but it is just as well to remember that in modern times, Darwinism, in at least a partial sense, has remained an important theory (or, better still, hypothesis) of evolution. Opponents there are, of course, and many biologists who do not agree with the philosophical implications of the theory still remain selectionists for want of a better working tool. A glance at a recent symposium on natural selection in the *Proceedings of the Royal Society*<sup>1</sup> will illustrate this general acceptance with modifications and will show that there are some disbelievers. For instance, Prof. R. Ruggles Gates<sup>2</sup> considers that natural selection has played a part in some cases of parallel evolution but not in all; C. Diver<sup>3</sup> holds a similar opinion in considering that species have formed as a result of several causes of which selection may be one; Prof. G. D. Hale Carpenter<sup>4</sup> considers that natural selection is the only theory that completely explains the problems of mimicry. Prof. E. W. MacBride<sup>5</sup> writes: "But it is obvious that selection by itself can produce nothing new". While finally J. B. S. Haldane<sup>6</sup> thinks that natural selection determines the evolutionary path which the species will take due to the appearance of mutations.

Natural selection, or the theory of the survival of the fittest, is essentially an explanation of the adaptation of organic things to their environment, and as such it may be a sufficient explanation; many biologists will accept this at its face value, because it is to a large extent self-evident. Nevertheless the theory of natural selection merely enunciates in scientific garb the truism that only those things survive that are *able* to live. The Darwinian theory, however, is not just concerned with the recognition that natural

<sup>1</sup> A Discussion on the Present State of the Theory of Natural Selection, Ed. by D. M. S. Watson, *Proc. Roy. Soc. B.* 121, 1936-37, pp. 43-73.

<sup>2</sup> *Ibid.*, p. 58.

<sup>3</sup> *Ibid.*, p. 65.

<sup>4</sup> *Ibid.*, p. 65.

<sup>5</sup> *Ibid.*, p. 70.

<sup>6</sup> *Ibid.*, p. 69.

selection is a force in nature, but also with the theoretical application of the operations of this force to the historical side of the subject, whereby it becomes seen, firstly, that inherited variations plus natural selection produce a selective death rate, and secondly, that this death rate can have an effect on the evolution of species. Both parts of the theory are really controversial, at least to some extent, for they are in some measure speculative.

The story of how Darwin and Alfred Russel Wallace simultaneously published the idea of natural selection as being the causal factor in the production of new species is too well known to be described in detail here. For twenty years previous to 1858 Charles Darwin had been working on his theory, then, unexpectedly, he received a communication from Wallace which embodied his own idea of natural selection. Darwin appealed for advice to Sir Joseph Hooker and, later, to Sir Charles Lyell. Finally it was agreed that joint papers by both Darwin and Wallace should be read before the Linnean Society by the secretary. This was done on the 1st July, 1858. At the Linnean Society Darwin-Wallace Celebration Meeting in 1908, the President, Dr. D. G. Scott, in reference to this meeting of 1858, said: "We are met together today to celebrate what is without doubt the greatest event in the history of our Society since its foundation. Nor is it easy to conceive the possibility in the future of any second revolution of biological thought so momentous as that which was started 50 years ago by the reading of the joint papers by Mr. Darwin and Mr. Wallace, *On the Tendency of Species to form Varieties: and on the Perpetuation of Varieties and Species by Means of Natural Selection.*"<sup>1</sup>

Both Darwin and Wallace had read Lyell's *Principles of Geology* and Malthus' *Essay on the Principles of Population* (1798); and both were influenced to a great extent by these books. From the first book they were strengthened in their general ideas that evolution was a fact and from the second they obtained the principles of the struggle for existence and the survival of the fittest. Darwin<sup>2</sup> tells us that he happened to read Malthus' book for amusement. Of this book Murray<sup>3</sup> says that everyone abuses it but no one reads it. Nevertheless, from long-continued observations of animals in their natural haunts, Darwin could appreciate the struggle for existence;

<sup>1</sup> The Darwin-Wallace Celebration, *Linnean Soc. of London*, 1908, pp. 1-2.

<sup>2</sup> F. Darwin: *Life of C. Darwin*, 1892, pp. 39-40, and *The Life and Letters of Charles Darwin*, Vol. I, 1887, p. 83.

<sup>3</sup> 1925, p. 173.

Malthus' application of the principles to man called forth in Darwin's mind the idea of natural selection as applied to wild animals and plants. Darwin says: "In October, 1838, that is fifteen months after I had begun my systematic enquiry, I happened to read for amusement *Malthus on Population*, and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observations of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved and unfavourable ones to be destroyed. The result of this would be the formation of new species."<sup>1</sup> And, again, in a letter to A. R. Wallace written in 1859, he says: "You are right that I came to the conclusion that Selection was the principle of change from study of domesticated productions; and then reading Malthus I saw at once how to apply this principle."<sup>2</sup>

Wallace in his *My Life, A Record of Events and Opinions*<sup>3</sup> tells us how as he was resting from an attack of fever something recalled to his memory Malthus' book on *Population*. His thoughts then turned from the affairs of human beings to those of animals where he thought that precisely similar conditions regarding survival exist. There is also an enormous destruction among animals. Further cogitation on this matter led him to consider: "Why do some die and some live? And the answer was clearly that on the whole the best fitted live. From the effects of disease the most healthy escape; from enemies the strongest, the swiftest, or the most cunning; from famine the best hunters or those with the best digestion; and so on. Then it suddenly flashed upon me that this self-acting process would necessarily *improve the race*, because in every generation the inferior would inevitably be killed off and the superior would remain—that is, *the fittest* would survive."

This recognition of the importance of Malthus' work by both Darwin and Wallace lends support to the view of Patrick Geddes<sup>4</sup> that the cra of scientific Darwinian theory is a reflection of the progress made in social evolution, and hence that biology becomes important as an educational introduction to the psychological and social studies. According to Geddes, Malthus' discovery of the struggle for existence caused by prevalent economic conditions

<sup>1</sup> *Life and Letters*, 1887, Vol. 1, p. 83.

<sup>2</sup> *Alfred Russel Wallace: Letters and Reminiscences*, James Marchant, Vol. 1, Letter 4, p. 136, 1916.

<sup>3</sup> 1905, London, Vol. 1, p. 361.

<sup>4</sup> See article on Biology in *Chambers' Encyclopadia*, Vol. 2, p. 162, 1901 Ed.

"have thus come to be temporarily exalted into a complete explanation of organic progress".

Other writers, such as W. C. Wells in 1813 and Patrick Matthews in 1831, had written about, or had conceived the idea of, natural selection. Darwin, however, knew nothing of their writings until after the publication of *The Origin of Species*, when they were brought to his notice. But neither Wells nor Matthews, nor any other person who perceived the possible operation of natural selection in nature, pursued the matter, or applied it in any way.<sup>1</sup> Darwin was undoubtedly the first to do this in a thoroughly comprehensive and systematic manner. Of the suggestion that new species may result from the operation of natural selection Huxley says: "But that suggestion is the central idea of the 'Origin of Species', and contains the quintessence of Darwinism."<sup>2</sup>

In 1859 Charles Darwin published his book setting forth in detail his new theory on *The Origin of Species by Means of Natural Selection and the Preservation of Favoured Races in the Struggle for Life*. The strength of the appeal of this work seems to lie in three things, which are detailed below.<sup>3</sup>

(a) The scientific world was uneasy about the question of immutability of species and the doctrine of special creation, which, admittedly, was founded rather upon a literal interpretation of Genesis, than upon scientific observations. As J. Huxley has it: "He was concerned both to establish the fact of evolution and to discover the mechanism by which it operated; and it was precisely because he established both aspects of the problem simultaneously that he was so successful."<sup>4</sup> In a word, the biological world, sceptical of special creationism, was waiting for the synthesis (which was also an analysis) that Darwin offered.

We may note here also that, unlike Lamarck and some of his other predecessors, Darwin did not, in *The Origin of Species*, draw up any formal pedigrees or schemes of classification, although he gave an account of the value and use of the classification of plants and animals. It was left to some of his followers to come forward with their phylogenetic schemes. In this respect Darwin merely contents himself with remarking ". . . that the nature of the relationship by

<sup>1</sup> It has been maintained that several others (such as Naudin in 1852, or James Watt in 1852) anticipated natural selection. See *Darwin and Modern Science*, Ed. A. C. Seward, Cambridge, 1909, pp. 13-17.

<sup>2</sup> *Life and Letters of Charles Darwin*, by F. Darwin, Vol. 2, p. 195, 1888.

<sup>3</sup> See Romanes, 1897.

<sup>4</sup> 1942, p. 173.

which all living and extinct beings are united by complex radiating and circuitous lines of affinities into one grand system, . . . all naturally follow in the view of the common parentage of these forms which are being considered by naturalists as allied, together with their modifications through natural selection, with its contingencies of extinction and divergence of character."<sup>1</sup> He calls this element of descent the only certainly known cause of similarity in organic beings. The *Origin of Species* then definitely sets forward the principle that the true natural classification represents a true genetic system among living things which sets animals and plants in a line, or lines, of blood relationship and based on similarity of morphological characteristics. This principle is still at the basis of all modern classifications. It is important to realise that it is an *assumption*, at least for the larger groups of organisms.

(b) Darwin's second appeal lay in his approach to the whole problem of scientific method. As Romanes<sup>2</sup> so ably points out, the "Bugbear of Speculation" was seriously retarding the true advancement of science (especially biological science) up to the beginning of the nineteenth century. This had been the work of the fertile imaginations of the Speculative Philosophers. Hence many naturalists confined their activities to the collection of dry facts and did not attempt to connect them together into a whole, or interpret the results of their findings, because they did not wish to be accused of speculation. Darwin, however, in his *Origin of Species*, sets a new style and method. No doubt he gives numberless facts in this book, but at the same time he presents them in such a way as to confound the reader and make it difficult for him to discern which are facts and which are assumptions.

Still, Darwin made use of his numerous facts in order to construct his theories in an attempt to discover the principles behind evolution. He differed from most of his predecessors in that his speculations and theories were *ultimately* founded on observations and not on his own imagination. He tried to verify his theoretical conclusions. Hence Darwin speculated freely on the one hand, but on the other hand he verified.

(c) Darwin's method of approach to the problem of species forms his third appeal. He first showed that species were mutable by bringing together evidence which indicated that domestic varieties of animal had been evolved by man. Thus he gave a detailed consideration to the origin of domestic pigeons, which

<sup>1</sup> *Origin of Species*, p. 489.

<sup>2</sup> 1897, Vol. 1, Intro., p. 2.

he showed had all been produced from the wild rock dove. His consideration of what a species *is* was left till after this. He then proceeded to introduce the idea of the struggle for existence which led on to natural selection. The extraneous evidences of evolution were then brought in. These are chiefly the geological, the morphological, geographical and anatomical considerations bearing on the subject. Throughout the book there is a wealth of illustration observed from nature which, of course, serves to strengthen his thesis.

According to Radl, Darwin took his logical method from Malthus, and indeed, he considers the *Origin of Species* to be written on the same pattern as the writings of the *laissez-faire* economists. Although Darwin considered that natural selection was the chief and most important cause of the evolution of species he never committed himself to say definitely what were the limits of its applicability. He recognised that other causal factors may be at work. The sentence<sup>1</sup>, "I am convinced that natural selection has been the main, but not the exclusive means of modification," admits of no hedging. It is the considered opinion of Darwin and, indeed, in successive editions of this book, as Herbert Spencer has shown, Darwin's faith in natural selection seems to have become less and less while his faith in the inheritance of the effects of use and disuse seems to have become greater and greater. In several places Darwin went to great pains to emphasize that use and disuse was a great factor in producing variations on which natural selection could work. This question was dealt with thoroughly in his *Variations of Plants and Animals under Domestication*.<sup>2</sup>

At the time of Darwin's death, Wallace was the only one who believed that natural selection was the sole causal agent in the evolution of species. Later, however, when Weismann brought out his germ plasm theory and the neo-Darwinian school arose, "Darwinism" came to mean "natural selection", in contradistinction to "Lamarckism" or "the inheritance of acquired characters".

### 3. DARWIN'S THEORY

#### (a) Variation

Any dullard can see for himself, if he takes the trouble to examine living things around him, that those of a single kind often vary. Variation is obvious, and it is equally obvious that these variations

<sup>1</sup> *Origin of Species*, Intro., p. 6.

<sup>2</sup> 1868, Vol. 2, p. 362.

have to live in certain surroundings, and in order to survive, must be adapted to these surroundings. Thus the environment, or the "conditions of life" as Darwin calls it, can act on varieties. It can act on the whole organism, or only on a part of it, or on the reproductive system.

Common experience shows us that species exist in nature, but still a species lacks precise definition. By studying various floras Darwin found that those genera possessing the larger numbers of individuals tend to increase still further in numbers, and so they increase the chances of leaving many more modified characters in their descendants. At the same time those genera with the larger number of species tend to become subdivided into subordinate groups. Thus nature would seem to be simultaneously building up and breaking down the same genera. This contradiction, however, may be more apparent than real for nature's delimitation of her species may not be based on the same criteria as those on which systematists base theirs. Her criteria may be more physiological than morphological.

Darwin pointed out that offspring from the same parent show slight variations and, although he knew that naturalists as a whole considered that these had little, if any, significant value as affecting the future history of the race, he was convinced that they formed the raw material on which natural selection worked. Before these minute variations could possibly influence the course of evolution, they must be inherited. Darwin merely assumed that they were inherited: he did not investigate the matter experimentally. This is surprising, for his whole argument depends on this point, and he was at great pains to collect examples to illustrate other parts of his thesis. Thus he wrote: "Owing to this struggle for life, any variations, however slight, and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to its physical conditions of life, will generally be inherited by its offspring." Darwin gives not the slightest evidence for this key phrase "will generally be inherited by its offspring"; indeed in this opinion he was actually flying in the face of experience.

#### *(b) Overproduction and the Struggle for Existence*

These two features are perhaps not so obvious as that of variation in nature. Darwin gives an example of a plant on the edge of a

desert which can be said to struggle for existence against an ever-recurring fear of drought. Apparently plants which vary in the direction of being able to resist drought, or to conserve water, have a better chance of surviving. This struggle for existence is a natural consequence of the fact that plants (and animals) produce more offspring than can possibly survive. "Every being which during its normal lifetime produces eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, or otherwise on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole of the animal and vegetable kingdom. . . ."<sup>1</sup>

### (c) *Natural Selection*

Natural selection is the crux of the Darwinian theory. The facts known are as follows:—

1. Variation—species do vary in nature.
2. Overproduction—there is overproduction among the vast majority of organisms; many more are produced than can possibly survive for the relative number of species in existence remains more or less constant.
3. Consequent upon this overproduction we may deduce that there is a struggle for existence.
4. Given variation and a struggle for existence then the main deduction of the argument follows, viz., that favourable variations in a given environment will tend to survive longer than the less favourable, and so will stand a better chance of propagating their kind. In a word they will be *naturally selected*. As Darwin says: "As many more individuals of each species are born than can possibly survive: and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a

<sup>1</sup> *Origin of Species*, p. 48.



better chance of surviving, and thus be *naturally selected*. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form."<sup>1</sup>

Darwin seems to have given no experimental illustrations of the operation of this principle of natural selection. Indeed in his chapter on the subject, his examples are purely imaginary. Under the hands of man artificial selection has proved a strong force in producing new varieties of organisms. Darwin asks the question whether or not this principle of selection could operate in nature also. He finds that it can and does. A point which Darwin emphasizes, first made by Hooker and Asa Gray, is that man, even with the organisms under his control, does not cause the origin of the variations on which he works through selection. All he can do is to take the fortunate variations as they occur, select and accumulate them. The same applies to natural selection. "Some have even imagined that natural selection induces variability, whereas it implies only the preservations of such variations as occur and are beneficial to the being under its conditions of life."<sup>2</sup> Herein, of course, lies the fundamental weakness of the whole theory. As variations are so common in nature it is reasonable to assume that some of them will possess sufficient advantage to ensure that they will be selected by nature and will be enabled to procreate their kind. This is the survival of the fittest. But Darwin is careful to point out that the term "natural selection" is only a metaphysical expression and must not be taken to mean an independent Power or Deity.

Throughout the *Origin of Species* there is a wealth of speculative illustrations of cases which may be explained by means of natural selection.<sup>3</sup> One of the chief factors leading to the action of natural selection is that of changed conditions in the environment caused by some such agency as climate. Variations favourable to the new environmental conditions would then be selected and those unfavourable to them would be weeded out. However, before a selected favourable variation can affect the evolution of the species concerned, it is necessary for new varieties in the same direction to be continually produced.<sup>4</sup> The change produced in the environment must also be continuous otherwise the new variety would revert back to its former condition.

<sup>1</sup> *Origin of Species*, pp. 4-5.

<sup>2</sup> *Origin of Species*, p. 84.

<sup>3</sup> The evidence for the occurrence of natural selection is given in a later chapter.

<sup>4</sup> *Origin of Species*, p. 89.

There is a very large literature on this part of Darwinism extending from 1859 to about 1870 and onwards. Not much is to be gained by going through this controversial period systematically. Suffice it to say, as already pointed out, that the Darwinists at first won the day. The decline in popularity of the theory arose later, not so much from the inadequacy of natural selection considered as a complete causal agent in the operation of evolution, but rather as a reaction to the materialistic approach to the whole subject of evolution.

It is proposed, therefore, in the following sections of this chapter to follow the method already adopted of examining the views of outstanding biologists of the period, not necessarily in chronological order. In biological writings generally an undue emphasis seems to have been laid on the opinions of those who were supporters of Darwinism, while many of the more important critics of the theory were all but ignored.

#### 4. THE RECEPTION OF DARWINISM

The first edition of *The Origin of Species* sold out on the very first day of its publication. Immediately, the theory became widely publicised by men like T. H. Huxley (who was perhaps Darwin's ablest advocate), Lyell, the geologist, and Hooker, the botanist. Opposition was soon forthcoming from the anatomist Owen, from the zoologist Mivart, and, because of its mechanistic bias, from certain clergymen. Thus a violent controversy ensued. As far as the opposition from clergymen is concerned, it would have been better if they had held their peace until the scientific critics at least had had time to load their guns for an attack, for their criticisms were mainly ill-informed and hastily conceived. This is well illustrated by the remark which T. H. Huxley made to Sir Benjamin Brodie in reference to the speech of Bishop Wilburforce at the British Association Meeting on June 30th, 1860, when he said: "The Lord hath delivered him into my hands."<sup>1</sup> The furore raised by the publication of Darwin's famous book is probably quite unique in the whole history of science. Although many reasons have been given for this (some of which have been mentioned already) it is still most difficult to decide what was at the back of it all. As in all cases where violent controversy reigns, the truth sank into the background for a time.

<sup>1</sup> See *Thomas Henry Huxley*, by J. R. Ainsworth Davies, English Men of Science Series, London, 1907, p. 53.

A study of the Darwinian and anti-Darwinian literature from 1860 onwards forces two outstanding features upon the mind. The first is the existence of a general *confusion* of thought. Writers wrote about Darwinism when they meant evolution and about evolution when they meant Darwinism. Darwin himself did little to dispel this cloud. Confusion often arose in another way, for some writers generalise about a *species* on the basis of changes noticed in an *individual*. Or, again, when discussing teleology and purpose in relation to Darwinian teachings, different writers give different meanings to these words as in T. H. Huxley's criticisms of Prof. A. von K  lliker's attack on Darwinism.<sup>1</sup> The second feature is that Darwin (or at least his followers) claimed to put forward a scientific idea in a scientific manner (this much is clear from the very way in which *The Origin of Species* is written), when in actual fact no experimental evidence was forthcoming in support of Darwin's theory. Its appeal was purely intellectual. In the scientific literature of this period we continuously come up against arguments and conclusions based on the following method of reasoning—such or such a condition in the natural world can be explained by means of natural selection, therefore natural selection is the guiding influence in nature. Agassiz<sup>2</sup> was probably hinting at this when he wrote: "The origin of all the diversity among living beings remains a mystery as totally unexplained as if the book of Mr. Darwin had never been written, for no theory unsupported by fact, however plausible it may appear, can be admitted in science". Agassiz' was a lonely voice, however, for still the theory was admitted.

T. H. Huxley considered *The Origin of Species* to be logically conceived and written but the Duke of Argyll thought it illogical. Many of Darwin's critics misunderstood Darwin's teaching,<sup>3</sup> but, on the other hand, many of his supporters misunderstood the criticisms. In such an atmosphere of controversy there was no room for compromise, a biologist, or indeed any educated person, was forced to be either Darwinian or anti-Darwinian *in toto*. As Radl says: "Today, when we look back upon these old criticisms of Darwin's views and the answers given by his supporters, it soon becomes obvious that here there are two opposing worlds of thought speaking different languages."<sup>4</sup>

<sup>1</sup> In *Darwiniana*, "Criticisms of *The Origin of Species*," pp. 82 *et seq.*

<sup>2</sup> 1860, p. 222.

<sup>3</sup> See Romanes, 1897, Vol. I, Chapter 9.

<sup>4</sup> 1930, p. 63.

Darwin took his cue from Kant and widely assumed that a close affinity between species meant a community of descent among them. It looked as though Darwin had discovered evolution, for up to the publication of the third edition he practically ignored the work of his predecessors in this field of biology. This point is argued extensively by Samuel Butler in his *Luck or Cunning?* Butler writes: "Buffon planted, Erasmus Darwin and Lamarck watered, but it was Mr. Darwin who said 'That fruit is ripe', and shook it into his lap."<sup>1</sup> Darwin did this so expertly that he persuaded people that he had produced a new theory of creation at a time when the old one was much the worse for wear.<sup>2</sup> In this way he disposed of the old doctrine of the immutability of species which led to a complete change in the methods of biological research, for the study of biology now became historical, not statistical.<sup>3</sup>

The evidences that Darwin brought forward to establish the theory of evolution were cumulative. He drew them from different branches of natural science, such as morphology, anatomy, embryology and also geographical distribution. In this manner, by piecing together the evidences from such varied fields of science, the final conclusion that species had indeed evolved from pre-existing species was considered to be proved. Previously Wallace had suggested that geological and geographical distributional evidence pointed to such a conclusion.<sup>4</sup> Darwin, in effect, united two basic principles of biology, for the idea of "unity of plan" in the organic world and that of "affinity" now came to denote genealogical, or genetical, kinship. Darwin had by no means been the first to do this, but he popularised it and this was no doubt due to the fact that at the same time as he made out a case for evolution he brought forward a theory of how evolution had occurred. On the face of it, the theory of natural selection was anti-teleological,<sup>5</sup>

<sup>1</sup> 1920, p. 247, 2nd Ed.

<sup>2</sup> For instance, see J. A. Lowell in the *Proc. of the American Academy of Sciences*, Vol. 4, 1860, p. 478, who says: "It is because he (i.e. Darwin) has unfolded a new theory of creation, that his views are espoused or combated with so much zeal. His facts are apparently, for the most part, uncontroverted; and it is precisely this admission of the facts that takes the inquiry from the exclusive domain of science, and opens it to all who are qualified to examine it merely as a deduction from acknowledged facts."

<sup>3</sup> See Marquis of Salisbury's Pres. Addr. to British Assoc., 1894.

<sup>4</sup> See Paper given by Wallace and quoted from in Appendix to Chapter 6.

<sup>5</sup> Later writers have not subscribed to this contention; for instance, in 1924 Berg wrote: "Selectionism must thus, from the outset, acknowledge the occurrence in the organism of purposive faculties in the shape of heredity, variation and self-preservation." (Berg, L. S., *Nomogenesis, or Evolution Determined by Law*, trans. by Rostovtsov, London, 1926, p. 18.)

and seemed to ascribe the production of new species of organisms to the operation of purely natural forces working haphazardly. No inner urge, no propelling force, was necessary to account for the change of species in the living world. Previously Descartes in his philosophy had separated mind from matter, while Kant had excluded teleology from science. Now, Darwin contended that evolution occurred haphazardly through the operation of purely mechanical causes. Biology had gone a stage further in its separation from metaphysics. As T. H. Huxley puts it, the path Darwin bids us follow "professes to be not a mere airy track, fabricated of ideal cobwebs, but a solid and broad bridge of facts. If it be so, it will carry us safely over many a chasm in our knowledge, and lead us to a region free from the snares of those fascinating but barren virgins, the Final Causes, against whom a high authority has so justly warned us."<sup>1</sup> And such was the temper of the times that this was thought to be a good thing. From a later but equally eminent German biologist, namely Weismann, we have a similar confession of faith that the great virtue of the Darwinian theory of natural selection lies in its exclusion of Design. Weismann says: "We accept natural selection not because we are able to demonstrate the process in detail, not even because we can with more or less ease imagine it, but simply because we must—because it is the only possible explanation that we can conceive. We must assume natural selection to be the principle of the explanation of the metamorphosis, because all other apparent principles of explanation fail us, and it is inconceivable that there could yet be another capable of explaining the adaptation of organisms without assuming the help of a principle of design."<sup>2</sup>

In the early days of the Darwinian Theory the supporters triumphed over the dissidents. Since that time the idea of organic evolution has been accepted by many biologists. For it was an idea that developed through the ages. With Darwin's popularisation the idea became firmly entrenched as a principle. With the new principle laid out before them in so brilliant a fashion as was done by Darwin and Huxley (to mention only two of the most famous evolutionists) biologists began to change their methods of research into the problems of the biology of species. Naturally enough, at once the value of the new principle was shown, for many

<sup>1</sup> Collected Essays, *Darwiniana*, 1893, p. 11.

<sup>2</sup> Quoted from Marquis of Salisbury's Pres. Addr. to B. A., 1894.

new facts became known and when generalised in the new fashion a new light was thrown on many hitherto obscure points. Darwin by his book threw over the subjective and *a priori* reasoning methods in science. But it happened that at the same time as Darwin established the theory of evolution he put forward his causal theory of natural selection. Having accepted the general theory, it was easy for biologists to accept natural selection. And so it was that Darwinism became widely accepted soon after the publication of *The Origin of Species*.

Since that time, however, biologists have learnt to distinguish clearly between evolution and the theory of natural selection, with the result that an ever increasing number of objections to the latter theory have been put forward from time to time, and many of them have never been satisfactorily answered. With the turn of the century the position was such that Kellogg, in 1907, after a most exhaustive analysis of the theory, could remark: "But Darwinism, as the all-sufficient or even most important causo-mechanical factor in species-forming, and hence as the sufficient explanation of descent, is discredited and cast down."<sup>1</sup> With the coming of Mendel and the newer knowledge of biology it has been said that Darwinism has been reborn in the present era of the twentieth century. But one of the foremost of modern "Darwinists" can only say of this matter: "The Darwinism thus reborn is a modified Darwinism, since it must operate with facts unknown to Darwin; but it is still Darwinism in the sense that it aims at giving a naturalistic interpretation of evolution, and that its upholders, while constantly striving for more facts and more experimental results, do not, like some cautious spirits, reject the method of deduction."<sup>2</sup> This sentiment seems to echo Weismann.<sup>3</sup>

In England Darwin was supported by T. H. Huxley, Hooker, Mill, Buckle, Romanes, Lyell, Wallace and others. T. H. Huxley

<sup>1</sup> 1907, p. 374.

<sup>2</sup> J. S. Huxley, 1942, p. 27.

<sup>3</sup> It is impossible here in the space at our disposal to discuss the writings of the many biological and other writers who wrote for or against Darwin's theory. All we can do is to give some general mention of the opinions of the times. For a very full treatment of the subject the reader can do no better than read Kellogg's *Darwinism Today* (1907). Kellogg deals very fully indeed with the theory itself and with its pros and cons and gives a final summing up representing the state of opinion towards the end of the first decade of this century. For earlier full treatments see Romanes' *Darwin and After Darwin* (1897) and the works of Alfred Russel Wallace. (See Bibliography for list of Wallace's Works.) The most complete and searching work on the subject is probably A. Wigand's *Der Darwinismus und die Naturforschung Newtons und Cuviers* (1874).

was undoubtedly the person in this country who was responsible for the wide acceptance of the theory. A clear writer and a wise and quick-witted debater, the sheer weight of his personality seems often to have given his arguments greater force than they perhaps deserved. He was Darwin's advocate at the time when little distinction was made between evolution and Darwinism. He scored against many of his biologically ill-informed critics, like Bishop Wilburforce, but against some of the more able and scientifically distinguished critics such as Mivart, he did not fare so well. At first he supported the theory for the sake of its scientific value. In his first essay on the subject<sup>1</sup> Huxley rejects the creation of species by fiat and the idea that species are immutable and gives his support to their evolution by natural means. He considers natural selection to be the only reasonable explanation of what these natural means are. Still, he bids investigators be cautious when he says: "It is doubt which so loves truth that it neither dares rest in doubting, nor extinguish itself by unjustified belief; and we commend this state of mind to students of species with respect to Mr. Darwin's or any other hypothesis as to their origin."<sup>2</sup> In his next essay<sup>3</sup> Huxley, because of the popularity and notoriety given to Darwin's book, takes upon himself the rôle of interpreter of the new theory. From this time on, there is a succession of papers and speeches in support of Darwin given to both scientific and popular audiences. His writings, however, gradually became infected with the materialism which led to his agnosticism. He himself lost the caution which he had earlier advised his contemporaries to exercise. In his criticism of Mivart's *Genesis of Species* he says: "In addition to the truth of the doctrine of evolution, indeed, one of its greatest merits, in my eyes, is the fact that it occupies a position of complete and irreconcilable antagonism to that vigorous and consistent enemy of the highest intellectual, moral, and social life of mankind—the Catholic Church."<sup>4</sup> The bias of such a statement is obvious, especially as it comes from a man who claims to have digested the works of Suarez, one of the greatest of theologians, in an afternoon. The statement further gives a clue to the motives behind Huxley's later evolutionary activities.

Mivart was strictly correct and perfectly justified in exclaiming:

<sup>1</sup> *Darwiniana*, 1859.

<sup>2</sup> *Ibid.*, 1859, p. 20.

<sup>3</sup> *Ibid.*, 1860.

<sup>4</sup> *Ibid.*, p. 147.

"If the *odium theologicum* has inspired some of its (i.e., Darwinian) opponents, it is undeniable that the *odium antithologicum* has possessed not a few of its supporters."<sup>1</sup>

It has been said that Darwinism found its spiritual home in Germany under Haeckel and later Weismann, and it was indeed supported by many famous German biologists, including Vogt, Buchner, Rolle, Preyer, Gegenbauer, Lange, Schmidt and Krause, to mention only a few.<sup>2</sup> Unfortunately the theory became entangled with the theories of the Social Democrats and soon assumed a materialistic aspect which the State considered to be so anti-social as to deprecate its teaching in the schools. The German biologists were determined to develop the theory to its uttermost logical conclusions even if this did lead to anarchy. Radl<sup>3</sup> writes: "By this time (1877) it was generally recognised that in Germany Darwinism represented, if not a new religion, at least a new faith."

In France, the reaction to Darwinism was quite different. The tradition of Cuvier, who had said that no science of natural history was conceivable unless species were stable, still persisted, and so the mass of French scientists, such as de Quatrefages, Milne-Edwards, Brogniart, Barroude, Claude Bernard, Flourens, were opposed to both the idea of evolution and to the theory of natural selection. Even in 1870 there was still considerable hostility to Darwinism. Evidence for this is provided by the treatment of the proposal that Darwin should be elected a member of the French Academy of Science in 1870.<sup>4</sup>

As we have already stated, the publication of *The Origin of Species* ushered in a period of controversy. Many biologists of the older school of thought, like Owen in England and Agassiz in America, never came to accept the theory. In fact, there never has been a lack of able critics of the Darwinian theory from 1859 up to the present. Kellogg<sup>5</sup> gives the following inspiring list of names of famous anti-Darwinians:—(a) earlier critics—von Baer, von K lliker, Virchow, N geli, Wigand and Hartmann, (b) later critics—von Sachs, Eimer, Delage, Haacke, Kassowitz, Cope, Goette, Haberlandt, Henslow, Wolff, Driesch, Packard,

<sup>1</sup> *Genesis of Species*, 1871, p. 12. A complete list of Huxley's writings can be found in J. R. Ainsworth-Davies' *T. H. Huxley*, Men of Science Series, London. Some are given in the Bibliography.

<sup>2</sup> A good but short account of Darwinism in Germany is given by Radl (1930), Chapter 4.

<sup>3</sup> 1930, p. 52.

<sup>4</sup> See *Nature*, Vol. 2, 1870, 261, 298, and 309.

<sup>5</sup> 1907, page 26.



Morgan, Haeckel, Steinman, Korschinsky and de Vries. To this list we can add the Englishmen Mivart, Samuel Butler, and the Duke of Argyll, the American Agassiz, the Frenchmen d'Archaic, de Quatrefages, Flourrens and the Germans Leydig, Braun, Wagner and Zockler, who gave a theological criticism.

It is intended now to give accounts of three different types of criticism of the Darwinian theory as follows:—(a) Mivart's famous criticisms treated as a whole, (b) Jenkins' criticism, which probably did more to weaken Darwin's position than any other single criticism, and (c) Korschinsky's unique method of criticism.

Mivart has been chosen for detailed treatment firstly in order to put before the reader the type of really damaging criticism which eventually led to a decline in the popularity of Darwinism; secondly because Mivart was one of the first really accomplished critics of the theory in this country; thirdly because he has often been scantily treated by those Darwinians who only too often ignored, or tried to laugh out of court, those who differed from them; and fourthly because Mivart gave a special treatment of the relation (supposed or real) between evolution and religion.<sup>1</sup>

## 5. CONTEMPORARY CRITICISMS OF DARWINISM<sup>2</sup>

### (a) Mivart's "*The Genesis of Species*"<sup>3</sup>

In editions of *The Origin of Species* subsequent to the publication of *The Genesis of Species* Charles Darwin deals at great length with

<sup>1</sup> The attacks on Darwinism began almost immediately. But most of the critics attacked Darwin in single papers only; Mivart was apparently the first biologist who kept up a sustained attack on the theory. For instance, Darwin himself wrote as follows to A. R. Wallace early in 1860 remarking on the incessant attacks made on their joint theory. He wrote: "Sedgwick and Prof. Clarke attacked me savagely at the Cambridge Philosophical Society, but Henslow defended me well, though not as a convert. Philips has since attacked me in a lecture at Cambridge; Sir W. Jardine in *The Edinburgh New Philosophical Journal*, Wollaston in *The Annals of Natural History*, A. Murray before the Royal Society of Edinburgh, Houghton at the Geological Society of Dublin, Dawson in *The Canadian Naturalists Magazine*, and many others. But I am getting case hardened, and all these attacks will make me only more determinedly fight. Agassiz sends me personal civil messages, but incessantly attacks me; but Asa Gray fights like a hero in defence; Lyell keeps as firm as a tower, and this autumn will publish on the Geological History of Man, and will then declare his conversion, which now is universally known. I hope that you have received Hooker's splendid essay. So far is bigotry carried that I can name three botanists who will not even read Hooker's essay!" (See *Alfred Russel Wallace, Letters and Reminiscences*, by James Marchant, Vol. 1, 1916, Letter 8, p. 142.)

<sup>2</sup> Those who wish to pursue further the topic "*The Reception of Darwinism*"

Mivart's criticisms of the theory of natural selection. *The Collected Life and Letters of Charles Darwin* also shows that Darwin attached great importance to Mivart's attack on the theory. Just after the publication of Mivart's book we find Darwin writing to Wallace of the distress caused to him by Mivart. He wrote: "I wish I had your power of arguing clearly. At present I feel sick of everything, and if I could occupy my time and forget my daily discomforts or little miseries I would never publish another word."<sup>1</sup> Like *The Origin of Species*, the *Genesis of Species* contains a wealth of illustrative examples, and the author, besides completely rejecting Darwinism as the causo-mechanical explanation of the origin of species, gives his own views, although he cannot be said to have put forward a definite theory of the origin of species. The book is a clever mingling of scientific facts and philosophical reasonings which can well serve as a model of how this should be done.

According to Mivart, Lamarck's "crude theory" and the English interpretation of it in Chambers' *The Vestiges of Creation* had rather discredited a belief in organic evolution. Mivart is a thoroughly-going evolutionist, and while he acknowledges that natural selection is a factor in Nature<sup>2</sup> the objects of his book are, firstly, by means of examples to show that natural selection is only a secondary factor in evolution requiring to be supplemented by other much more important but as yet unknown laws. For he says: "If the theory of Natural Selection can be shown to be quite insufficient to explain any considerable number of important phenomena connected with the origin of species, that theory as the explanation must be considered as provisionally discredited."<sup>3</sup> And secondly, he wishes to show that there is no necessary antagonism between evolution and religion.

<sup>1</sup> *Alfred Russel Wallace: Letters and Reminiscences*, by J. Marchant, Vol. 1, p. 268. Letter written to Wallace, July 12th, 1871.

<sup>2</sup> At first Mivart was inclined to believe in the theory.

<sup>3</sup> 1871, p. 19.

---

should read the *Life and Letters of Charles Darwin*, by F. Darwin, 1888, especially Vol. 2. Here much information about those who supported Darwin's theory can be obtained. Chapter V, by Prof. T. H. Huxley, although not without serious faults, is illuminating in this respect. Here in this account of Darwinism, for reasons already mentioned, and also because, historically speaking, critics reflect the reactions of their times perhaps even more so than the supporters of a theory, it was decided to concentrate on giving a more or less detailed account of the writings of some of the more important critics.

<sup>3</sup> An excellent, but unfortunately incomplete, review of this book by A. W. Bennett will be found in *Nature*, Vol. 3, 1871, 270-273.

The difficulties confronting acceptance of Darwinian theory are summed up by Mivart as follows:—

1. That natural selection is incompetent to account for the incipient stages of useful structures.

2. That it does not harmonize with the co-existence of closely similar structures of diverse origin.

3. That there are grounds for thinking that specific differences may be developed suddenly instead of gradually.

4. That the opinion that species have definite though very different limits to their variability is still tenable.

5. That certain fossil transitional forms are absent which might have been expected to be present.

6. That some facts of geographical distribution supplement other difficulties.

7. That the objection drawn from the physiological difference between "species" and "races" still exists unrefuted.

8. That there are many remarkable phenomena in organic forms upon which "natural selection" throws no light whatever, but the explanations of which, if they could be attained, might throw light upon specific origination.

These objections are amplified below.<sup>1</sup>

The theory of Darwin postulated the occurrence of minute variations which are continually naturally selected over a long period of time until a new species emerges. Mivart contends that "no mere survival of the fittest accidental and minute variations can account for the incipient stages of useful structures, as for example the structures which led to the production of the heads of flat fishes, the baleen of whales, the limbs of vertebrates, the laryngeal structures of the new-born kangaroo, the pedicellariæ of echinoderms, or for many of the facts of mimicry" (for example in the production of such wonderful mimics as *Kallima*, the leaf-butterfly, or the walking leaf insect) "and especially in those last touches of mimetic perfection where an insect not only mimics a leaf, but one worm-eaten and attacked by fungi."<sup>2</sup> Further, the origination of structures like the hood of the cobra, the rattle of the rattlesnake, colours of some apes, beauty in some shell fish, the origin of the eye, and the refinements of the human

<sup>1</sup> Mivart, in his Chapter on "Specific Genesis", himself gave an admirable summary of his objections and one can do no better than to transcribe these almost verbatim, from the author's own words. This has been done in the text.

<sup>2</sup> 1871, p. 220.

ear and voice cannot all be explained solely by the action of natural selection.

As regards the second objection, on a non-Darwinian theory of evolution, the development of closely similar structures of diverse origin might be expected on *a priori* grounds. It is very difficult to imagine how they could independently arise by the natural selection of minute fortuitous variations. There are examples of close similarity of animal organs between which there could be no genetic affinity, such as the same eye structure found in vertebrates and molluscs described by J. J. Murphy.<sup>1</sup> "A curious resemblance, though less in degree, has also been seen to exist between the auditory organs of fishes and of cephalopods" and also "remarkable similarities between certain placental and implacental mammals, between the bird's head processes of *polyzoa* and the pedicellariæ of echinoderms, between *ichthysauria* and *cetacea* have been found." Certain groups of animals seem to possess an inborn tendency to develop some particular feature along a certain line such as beauty and singularity in the birds of paradise. Or, again, similarity may be directly induced by obscure causes such as geographical distribution, as in the loss of the tail in some butterflies. Cases like these, Mivart contends on good grounds, are inexplicable by the natural selection of minute variations.

Mivart brings forward some evidence of specific differences which arise suddenly as sports. In the interval of such changes the species concerned remains stable. As some examples he gives the English oysters, which when transferred to the Mediterranean immediately changed their mode of growth, becoming similar to the indigenous ones, and also the Normandy pigs which sometimes develop curious jaw appendages. Besides these there are also the examples of the Ancon sheep, black shouldered peacocks, many vegetable varieties and a multitude of other widely diverging forms which have all been described as appearing suddenly and not by the accumulation of minute changes. Mivart gives "the labyrinthodon, the hand of the potto, the whalebone of whales, the wings of birds, and the climbing tendrils of some plants" as examples of structures which in all probability originally appeared suddenly. "It has also been shown that certain forms which were once supposed to be especially transitional and intermediate (as, e.g., the aye-aye) are really by no means so; while the general

<sup>1</sup> *Habit and Intelligence*, Vol. 1, p. 321.

rule that the progress of forms has been "from the more general to the more special has been shown to present remarkable exceptions, as e.g., *Macrauchenia*, the glyptodon and the sabre-toothed tiger". Such facts as these are not irreconcilable with natural selection but only tell against it.

Next, as to specific stability, it has been seen that there may be a certain limit to normal variability, and that if changes take place they may be expected *a priori* to be marked and considerable ones, from the facts of the inorganic world, and perhaps also of the lowest forms of the organic world. It has also been seen that with regard to minute spontaneous variations in races, there is a rapidly increasing difficulty in intensifying them, in any one direction, by careful breeding. Moreover, it has appeared that different species show a tendency to variability in special directions, and probably in different degrees, and that at any rate Darwin himself concedes the existence of an internal barrier to change when he credits the goose with "a singularly inflexible organization"; also that he admits the presence of an *internal* proclivity to change when he speaks of a whole organization seeming to have become plastic, and tending to depart from the parental type!

As regards the fossil evidence which Darwin puts forward as strong evidence in favour of evolution, Mivart objects that "we have as yet no evidence of minutely intermediate forms connecting uninterruptedly together undoubtedly distinct species" as we could reasonably expect to have on the Darwinian theory. In the older strata according to Darwinism life must have been abundant and varied. "All the most marked groups, bats, pterodactyls, chameleons, *ichthyosauria*, *anura*, etc., appear at once upon the scene." Even the horse with the best preserved pedigree does not give any real conclusive evidence of evolution by accumulation of minute changes. Such difficulties are avoided if we allow that new forms of life appeared by natural means but more or less suddenly.

The question of Time also enters in here. For if evolution has occurred according to the Darwinian method, an incredibly long period of time would be necessary—a far greater number of years than the greatest estimate of the age of life on the earth.

Some of the facts of geographical distribution are difficult to explain on a Darwinian basis, but these can only be admitted as evidence when taken in conjunction with other stronger objections. As Mivart says: "These facts, however, are not opposed to the doctrine of evolution; and if it could be established that

closely similar forms had really arisen in complete independence one of the other, they would rather tend to strengthen and support the theory".<sup>1</sup>

The facts of homology "are not explicable without admitting the action of what may most conveniently be spoken of as an internal power, the existence of which is supported by facts not only of comparative anatomy, but of teratology and pathology also. "Natural selection also has been shown to be impotent to explain these phenomena, while the existence of such an internal power of homologous evolution diminishes the *a priori* improbability of an analogous law of species origination."<sup>2</sup>

Thus Mivart by his well substantiated objections does not deny the existence of natural selection, but he brings forward a cumulative argument against its efficacy as a chief explanation of the evolution of species. Natural selection plays a part, but only a subordinate one, in the organic world. The next step is to consider whether some other *modus operandi* can be substituted for that of natural selection as the chief agent acting in evolution. And this Mivart proceeds to do. He finds that his researches and studies lead him to think that an internal force exists which is responsible for the evolution of species. None of the objections raised against the theory of Darwinism can be raised against this conception. This force is the dominant causal agent in evolution and works in conjunction with subordinate agents such as natural selection, reversion and heredity, etc. Mivart then builds up an elaborate theoretical argument in support of his idea and he replies at once to the obvious objection likely to be made against his theory by saying: "It will, however, be replied that such an entity is no *vera causa*; that if the conception is accepted, it is no real explanation; and that it is merely a roundabout way of saying that the facts are as they are, while the cause remains unknown. To this it may be rejoined that for all who believe in the existence of the abstraction 'force' at all, other than will, this conception of an internal force must be accepted, and located somewhere, it cannot be eliminated altogether; and that therefore it may reasonably be accepted in this mode as in any other."<sup>3</sup>

The merit of Mivart's theory of an "internal force" directing evolution lies in the fact that it enables him to bring back Intelligence

<sup>1</sup> 1871, p. 154.

<sup>2</sup> 1871, p. 224.

<sup>3</sup> 1871, p. 227.

to the theory of organic evolution which a materialistically interpreted Darwinism was attempting to get rid of.<sup>1</sup> His notion of such a force was forgotten to a great extent by his contemporaries, who preferred to remain indifferent rather than to meet or analyse his arguments in its favour. Nevertheless the notion of a life-force had again been publicised, this time by a competent biologist, and the idea grew. This was, of course, due to those who held to such conceptions, but it was also due in some measure to Darwin himself. It has been stated earlier that Darwin finally separated biology from formal metaphysics. This may be so, but with the introduction of evolution and the idea of natural selection he also opened up the way for a newer departure from the dualism of Descartes. According to Descartes, nature comprises matter and mind, but now the idea of a life force—a vital energy—could definitely come in to philosophical biological reasonings, even though it did receive a new impetus from Darwin's purely mechanical theory of selection. For, in spite of Darwin's assertions, selection implies something which selects, some object outside the organism but working on it from within. This object is personified as "Nature". The idea of an entelechy is not new, but now, with the general acceptance of organic evolution and of Darwinism in particular, the conception has developed rapidly until we have Bergson's fully worked out idea of an *élan vital*. This has recently been pointed out by R. G. Collingwood, who says: "On the ground of philosophy, I think it is fair to say that the conception of vital process as distinct from mechanical or chemical change has come to stay, and has revolutionized our conception of nature."<sup>2</sup>

### (b) *Mivart on Evolution and Religion*

Because of undue materialistic interpretations<sup>3</sup> which have been put on evolutionary theories an account of the relation

<sup>1</sup> Mivart says: "Organic nature, then, speaks clearly to many minds of the action of an intelligence resulting, on the whole and in the main, in order, harmony and beauty, yet of an intelligence the ways of which are not such as ours." (1871, p. 238.)

<sup>2</sup> 1945, p. 136.

<sup>3</sup> For instance, Mivart writes: "The notion that the origin of species is due to 'Natural Selection' is a crude and inadequate conception which has been welcomed by many persons on account of its apparent fatal effects on a belief in Divine Creation. Its anti-teleological character has been declared by a conspicuous English advocate, to be 'one of its greatest merits', while it has been made use of as a fundamental dogma in the various polemical works of Professor Haeckel". (Mivart, *The Cat*, 1881, p. 520.)

between this scientific theory and religion is obviously historically necessary. One of Darwin's objects in writing *The Origin of Species* was to discredit the theory of special creation of species. All Christians are committed to the idea of "creation". Hence it was inevitable that a conflict should seem to exist between Darwin with his idea of evolution and those who believed in creation. Mivart carried out a large amount of historical research on the subject and his views remain sound and lasting, in fact they have scarcely been improved upon since he wrote them in 1871. The most recent full treatment of this subject is E. C. Messenger's *Evolution and Theology*.<sup>1</sup> This book is exhaustive in its treatment and scholarly in its presentation of the thesis and will no doubt become a classic. Readers who wish to study the subject further may be recommended to read it. This would seem to be an appropriate place at which to introduce the topic of "Religion and Evolution", and we can do this adequately enough by considering some of Mivart's views.

Mivart accuses Darwin of pandering to those attackers and defenders of the theory of natural selection who seem to think that it necessarily contradicts theism, or what is called special creation. Mivart contends that many distinguished Christian thinkers have accepted both of these ideas of "evolution" and of "special creation".<sup>2</sup> Even to this day this misunderstanding of the various meanings of the word "creation" still exist. Many of the "anti-theistic" Darwinians, when writing of creation, either used the word in its absolute sense, or led their readers to think that this was the only sense of the word.<sup>3</sup> Mivart then settles this confusion at once

<sup>1</sup> 1931, London.

<sup>2</sup> Referring to this important point, Mivart quotes "an eminently Christian writer," writing in the *Rambler*, March, 1860, as follows: "The creationist theory does not necessitate the perpetual search after modifications of miraculous powers and perpetual 'catastrophes'. Creation is not a miraculous interference with the laws of nature, but the very institution of those laws. Law and regularity, not arbitrary intervention, was the patristic ideal of creation. With this notion, they admitted without difficulty the most surprising origin of living creatures, provided it took place by *law*. They held that when God said 'Let the waters produce', 'Let the earth produce', He conferred forces on the elements of earth and matter which enabled them naturally to produce the various species of organic beings. This power, they thought, remains attached to the elements throughout all time." The same writer quotes St. Augustine and St. Thomas Aquinas to the effect that "in the institution of nature we do not look for miracles, but for the laws of Nature" (St. Thomas, *Summa*, 1<sup>a</sup> 2<sup>a</sup>, lxxvii, 4 ad 3). And again, St. Basil speaks of the continued operation of natural laws in the production of all organisms." (*Hexam Hom.*, ix, p. 81.) From Mivart, 1871, p. 17.

<sup>3</sup> Strictly speaking, science can say nothing about absolute creation, for science deals only with tangibles. It may be said that a conception of absolute creation



by stating the various meanings of the word "creation". Merely to do this is indeed to settle the dispute (real or imagined) between evolution and religion from this point of view. He describes three ordinary meanings to the word: (a) The absolute origination of anything out of nothing—this is *absolute creation*—and, of course, implies the direct operation of the Creator. Furthermore, it is beyond the scope of materialism to deal with this at all because of its basic premises; (b) *Derivative creation* where matter has already been created in the absolute sense and further endowed with a potentiality to evolve or change later; (c) *Creation by the hyper-physical action of intelligent man* making use of powers and laws previously given by God.

As far as evolution is concerned it is derivative creation which is meant when the theist speaks of God as creating all species. *Individuals* comprising the species are demonstrably produced by reproductive processes in a perfectly natural way, but the species has the innate power of reproducing in its characteristic way without direct intervention from the Creator of that power. Derivative creation is the creation through the action of secondary causes, which, so far as evolution is concerned, are perfectly natural causes. There is then no real contradiction, or conflict, between evolution and the dogma of creation on this issue.<sup>1</sup>

Mivart says: "Now much confusion has arisen from not keeping clearly in view this distinction between *absolute* creation and *derivative* creation. . . . The greater part of the apparent force

<sup>1</sup> It is just as well to remember here what a dogma really is. It is a truth established by the use of reason, which, if we believe in reason at all, we must accept. The passage of years does not alter its truth, new discoveries in science do not vitiate it. As far as religion is concerned, a dogma may be revealed, or established by reason alone. (If it is established by revelation we still use our reason in arriving at the revelation, but it is at this point that faith often enters in.) Empirical science can say nothing about dogmas of this kind. To deny this would be to deny the power of human reason based on primary intuitions, and thus to take away the only basis we have for all our knowledge—whether physical, theological or metaphysical, which, of course, would lead to absolute scepticism. The dogma of creation is a necessary dogma for the theist, and it is established by means other than experimental. This is not to say that empirical science cannot bring forward confirmatory evidence to clarify the meaning of the dogma, or show how it is brought about in the material world, but only that this branch of science can neither affirm nor refute it.

---

is valueless, for it is inconceivable, and even unimaginable. Against such statements we may quote Mivart as follows: "That it is 'conceivable' is proved by the fact that it is widely, not only conceived but believed. That it is 'unimaginable' necessarily follows from its being an act which, by the hypotheses, is utterly beyond experience." (*Lessons from Nature*, 1876, p. 371.)

possessed by objectors to creation, like Mr. Darwin, lies in their treating the assertion of derivative creation as if it were an assertion of absolute creation, or at least of supernatural action. Thus he (i.e., Darwin) asks whether some of his opponents believe that at innumerable periods in the earth's history, certain elemental atoms have been commanded suddenly to flash into living tissues.<sup>1</sup> Certain of Mr. Darwin's objections, however, are not physical, but *metaphysical*, and really attack the dogma of secondary or derivative creation, though to some perhaps they may appear to be directed against absolute creation only."<sup>2</sup> Mivart then proceeds to show that derivative creation is not a supernatural act, but merely Divine action through natural laws. Theists must necessarily hold that the creator acts in this way, while atheists must of necessity deny it, but they can never show it to be false by investigation of purely natural laws. Any conflict then between evolution and creation arises through misunderstanding of the meanings of these words.

Mivart, having shown that Christians are free to accept the idea of evolution, proceeds to inquire whether or not any theological authorities support the contention. In this connection he cites St. Augustine, St. Thomas Aquinas, and Suarez who was one of the most brilliant of the more modern theologians.<sup>3</sup> "It is then evident that ancient and most venerable theological authorities distinctly assert *derivative* creation, and thus harmonize with all that modern science can possibly require."<sup>4</sup>

Finally, Mivart passes on to consider the origin of man. The scholastic definition of man was that of an *animal rationale*. His animality is distinct in nature from his rationality, and each must then have had a different origin, so the author finds no difficulty in believing in the evolution of man's body in a perfectly natural way for, excluding the scientific evidence for this, the Scriptures would seem to affirm it, for we are told that "God made man from the dust of the earth" and then breathed into it "the breath of life". Man's body was thus made through the intermediary of "dust", that is to say, through the operation of secondary causes. The "breath of life", man's soul, his rational part, however, comes under a different mode of origin. Scripture indicates that it is

<sup>1</sup> *Origin of Species*, 5th Ed., p. 571.

<sup>2</sup> 1871, p. 254.

<sup>3</sup> E. C. Messenger in *Evolution and Theology*, a book already mentioned, deals in detail with all the important Early Fathers of the Church and theologians.

<sup>4</sup> 1871, p. 266.

distinctly and separately created in the sense of absolute creation. This idea of the double nature of man is not contradictory to anything that science teaches, inasmuch as man's rationality is hyper-physical. Mivart concludes "we have a true reconciliation of science and religion, in which each gains and neither loses, one being complementary to the other".<sup>1</sup>

### (c) *Jenkins' Criticism*

In 1867 Jenkins (1867, p. 309) gave a most devastating criticism of many points of the Darwinian theory. In particular, he pointed out that, given a favourable variation which was naturally selected, this variation would have no permanent effect on the species, because by breeding it would be swamped, and so soon lost. Darwin was aware of this criticism, and he considered it to be a fair one. Although heredity was a corner stone of his theory it was obviously a subject to which Darwin gave scant attention, for, referring to Jenkins' criticism in the 5th edition of *The Origin of Species*,<sup>2</sup> he says, "I did not appreciate how rarely simple variations, whether slightly or strongly, could be perpetuated". Some of the Darwinians attempted to overcome this objection by clouding the issue. For instance, in 1899, F. W. Hutton<sup>3</sup> assured us that Darwin later recognised "that natural selection acts, not by preserving a few high favoured individuals, but by killing off all those which do not come up to a certain standard." As if this settled the matter—the perpetuation of the advantageous variation has still to be accounted for and the effects of swamping still remain.

Thus neither Darwin nor any of his supporters were able to give a satisfactory reply to this criticism, which, if valid, destroys the foundations of Darwinian Theory. Even today the objection still stands.<sup>4</sup> The only solution is to deny that rare chance variations play any part in species forming, and to assert that natural selection acts only on variations produced in large numbers. But for Darwinians to do this is to confess to defeat, for the essence of true Darwinism is evolution by means of the natural selection of haphazard variations which chance to be useful to the individual.<sup>5</sup>

<sup>1</sup> 1871, p. 287.

<sup>2</sup> p. 104.

<sup>3</sup> *Darwinism and Lamarckism*, London, 1899, p. 3.

<sup>4</sup> See Willis, *Course of Evolution*, Cambridge, 1940.

<sup>5</sup> G. Pfeffer in *Die Umwandlung der Arten*, 1894, and G. Wolff in *Der gegenwärtige Stand des Darwinismus*, 1896, have both discussed the force of this objection very critically.

To advocate natural selection is not to advocate Darwinism, for the idea of natural selection was known and published before Darwin's time.

(d) *Korschinsky's Criticisms*

An extreme anti-Darwinian attitude is that taken up by the Russian Korschinsky,<sup>1</sup> who formulated a theory of evolution by means of saltations, which he called *Heterogenesis*. Korschinsky's views are important, because they are put forward by a noted botanist belonging to a school remote from England, and also because they represent a completely different and logical interpretation of facts similar to those recognised by Darwin. Further, Korschinsky set his opinions in direct contrariety to those of Darwin. This critic of Darwin who completely reversed the latter's theory founded his ideas on observation, and, like Darwin, he did little, if any, experimental work to support his contentions. The systems of both writers are largely intellectual. Korschinsky's treatment of the subject should serve as an object lesson of the danger of placing too much reliance on any single scientific theory which is not based primarily on experiment. Kellogg reminds us that "of exact proof, in the nature of observed fact or result of experiment, or of mathematical demonstration, there is little in the case either of the Darwinian or the Korschinkian interpretation".<sup>2</sup>

Darwin considered that small variations occurred regularly, and the advantageous ones among them are naturally selected. On the other hand, according to Korschinsky, all organisms possess an inherently-controlled capacity to vary. Normally such variations are not given off, but occasionally they arise as sudden changes, and under favourable conditions may form new species. Once formed, such new species do not evolve further except that occasionally new mutations may arise. The Darwinian view considers that all species vary persistently and advantageous ones are continually selected. Korschinsky recognised that there is a struggle for existence, but, in opposition to Darwin, he thought that the greater the struggle for existence, the slower evolution occurred. If new forms did appear under a severe struggle they would soon die off. According to Darwinian theory the more difficult the external conditions the quicker would occur

<sup>1</sup> *Heterogenesis and Evolution, Naturwiss. Wochenschrift*, 14, 273-278, 1899.

<sup>2</sup> Kellogg, 1907, p. 92.

the evolution of new species. A lack of competition, according to Darwinian ideas, would mean a halting of evolution. According to Korschinsky, it would result in the attainment of a perfected schema of evolution complete with all intermediate forms. Darwin concluded that evolution is the result of adaptation to external conditions, while Korschinsky concluded that evolution is a result of an innate tendency towards perfection which is practically identical with the tendency to vary.

## CHAPTER 6

### THE FORMULATIVE PERIOD CONCLUDED :

#### (D) AFTER DARWIN

##### I. THE ESTABLISHMENT OF EVOLUTION AS A PRINCIPLE

###### (a) *General Effects*

NATURAL selection gives a satisfactory explanation of how changes in species can be brought about in nature and, like Lamarckism, it appeals to common-sense. But the assumptions it makes are enormous;<sup>1</sup> the basic one is, of course, that slight continuous variations occur over a long period of time and are inherited. Natural selection, as Darwin says, works daily and hourly "at the improvement of each organic being in relation to its organic and inorganic conditions of life." This would seem to indicate only that individuals of succeeding generations are gradually rendered more and more adapted to their surroundings. It does not follow that any approach to perfection of adaptation attained by any individual, or group of individuals, necessitates a change in the nature of that individual, or group of individuals. In other words, if we assume that the differences separating species are deep-seated, affecting the whole organization of the individuals of that species, and are not merely superficial characteristics, then slight variations continuously occurring and continuously naturally selected may perhaps produce and perpetuate varieties, or races, of organisms but not necessarily species.

In spite of the severe criticisms of Jenkins and others, the success of *The Origin of Species* in the early years after its publication clearly established the idea of organic evolution as a principle of biology. At the beginning of the present century the only biologist of note, who openly disavowed organic evolution, was A. Fleischmann,<sup>2</sup> a professor of Zoology in the University of Erlangen. Scientifically the idea of evolution, that is, the idea of continuous progression

<sup>1</sup> Willis, 1940, pp. 167-168, for example, gives a list of 33 of what he calls the most important assumptions made by the theory of natural selection.

<sup>2</sup> 1907.

of organic forms through genetic connection, was as firmly accepted a law as that of gravitation. A hypothesis developed into a theory and the theory became accepted by many of its extreme advocates as a fact—as solid a fact as any which our human reason enables us to perceive. Biology thus became transformed, and a period of re-orientation set in. So that from this time till the end of the nineteenth century many new evolutionary ideas were brought forth. The philosophical implications of both the theory of organic evolution and the theory of natural selection spread from biology into anthropology, sociology and other pursuits. Biologists themselves were stimulated to look for *resemblances* between organisms in order to show the affinities of species, genera and even phyla of plants and animals. Many of the German Schools of Zoology accepted the theory wholeheartedly. At least, if they did not accept natural selection as the causal theory of evolution, they accepted the idea of evolution by small stages. Haeckel, for instance, was one of the most famous of continental evolutionists and probably did more than anyone else to popularise and force people to accept the theory of evolution. He was the “firebrand” of the evolutionary cause, but he did not accept natural selection as the chief cause of the changes in species.

Gradually biology became speculative again (without much real theoretical basis). This time the speculators were themselves biologists, but biologists imbued with an idea—the idea of evolution, not only of living things, but of the whole cosmos. Evolutionary theory became separated from physiology, the experimental side of biology. Inevitably the reaction set in, producing physiologists like Loeb, who reversed the Darwinian conception by attempting to show that function was of more importance than structure.

Loeb's method was essentially experimental; he worked on the lower animals such as echinoderms, worms and insects. Thus there arose the science of comparative physiology. Loeb's explanations, however, were purely mechanistic, for he sought to explain function in purely physico-chemical terms. Animals were considered merely as bundles of chemicals with certain physical properties.

Other physiologists returned to the teleological viewpoint and began again to look for purpose in the operations of the natural world. Darwin had separated the natural sciences from metaphysical bonds. Now with the arrival of Driesch and his revival of the notion of Aristotle's *entelechia*, and later Bergson's creative evolution, wherein is envisaged an *élan vital*, or driving force, in

life's processes, vitalistic as opposed to mechanistic explanations of life and evolution reappeared on the scene. This attack on Darwinism, which first arose as a reaction against the over-emphasis on morphology and later against the mechanistic interpretations of biology, went hand in hand with an attack from a different point of view. We have seen that the essence of the Darwinian theory is that evolution proceeds by the gradual accumulation of small and favourable variations which are continuously naturally selected. The cumulative effect of this is gradually to change a species into a new one. Evolution is then a continuous process, and the variations also are continuous from generation to generation. It was well known, however, that many variations are not continuous but arise from the present organism at a jump, producing sports, or mutations as we call them now. In 1894 Bateson published his *Materials for the Study of Variation*, a large work in which are gathered numberless examples of discontinuous variations of this kind. This work probably led to the formulation of the mutation theory of evolution by de Vries in 1900. De Vries worked on *Oenothera*, the evening primrose, and put forward the contention that these large jumps, or mutations, were the raw material on which evolution worked.

We have now just seen how the theory of evolution more or less definitely supplanted the theory of special creation by about 1870 and we have also seen how, while biologists accepted evolution, they did not all accept natural selection as the causal agency. These latter workers then turned to the only other causal theory extant at the time, i.e., to Lamarckism. Thus arose the school of neo-Lamarckians in opposition to the school of the neo-Darwinians, which received much of its inspiration from Weismann, who, by his theories of the germ plasm and germinal selection, supplied to Darwinian theory the much needed explanation of how variations were inherited. The basis of Weismann's theory is, of course, the cell theory first developed by Schleiden and Schwann which we have already considered.<sup>1</sup>

Many of the modern theories of evolution owe their inspiration to Weismann also, so that we will have to consider his work in some detail below. Weismann, like Darwin, postulated that the variations which counted in evolution were continuous. But the germ plasm theory could also be applied to explain the inheritance of discontinuous variations, especially after the rediscovery of

<sup>1</sup> See Chapter 4, Section 7.



Mendel's principles of heredity by de Vries, Correns and Tschermak in 1901. The early Mendelians traced the inheritance of large contrasted differences between organisms, and so it was but a step to consider that mutations, as being sharp and clear-cut distinctions from the original, were the variations which were really inherited. Up till then no one had shown that Darwin's small continuous variations were inherited at all. It is only in very recent years that evidence for this has been obtained.

Hence early genetical theory lent its weight to the mutation theory of evolution. In 1903 Sutton showed that the chromosomes were the bearers of the factors postulated by the Mendelians and much later, Peacock on the sawfly, and Muller on the Fruit Fly, developed the X-ray technique of producing small variations which were inherited in a Mendelian fashion. Once it became recognised that mutations could be small as well as large, the mutation theory became absorbed by the neo-Darwinians into the general theory of natural selection. A modern synthesis was then achieved.

#### *(b) Neo-Darwinism and Neo-Lamarckism*

Scientifically-founded criticisms, like those of Jenkins and Mivart already mentioned, were sometimes answered and sometimes ignored or glossed over. But, as they accumulated, their effects became obvious. A considerable body of informed biological opinion began to doubt the efficacy of natural selection as the only causal factor in the origin of species. The criticisms brought to light many cases which could not be explained by means of this factor, and so subsidiary theories were brought in to support it. The chief subsidiary theories supplementing that of natural selection are:—(a) a theory of sexual selection (1871), (b) the isolation theories (1868-72), (c) Roux's "battle of the parts" (1881), (d) the theory of organic selection (1896), and (e) Weismann's germ plasm theories (1895). Some biologists, however, did not accept natural selection as a causal factor in evolution, and offered theories of their own. The most important of these substitutionary theories are as follows:—(a) a revival of Lamarckism, (b) orthogenesis, and (c) heterogenesis. The introduction of heterogenesis, or mutation theory, brings us up to about 1901, when Mendel's principles of heredity were re-discovered, and this marks the end of our Period of Formulation of the Evolution Idea. Each of these theories will be dealt with in this chapter.

Darwin was very emphatic that natural selection, although the most important, was not the only causal factor in organic evolution. In *The Origin of Species* he recognised the importance of the Lamarckian factor of use-inheritance, while in his *Variations of Plants and Animals under Domestication* (1868) he devoted two chapters to the consideration of examples of use and disuse. His own position is best summed up in his own words given at the end of the introduction to his *Origin of Species*, where he says: "I am convinced that natural selection has been the main, but not the exclusive, means of modification." Nevertheless, Darwin never seems to have given much credit to Lamarck who first seriously propounded this idea of use-inheritance. Darwin, in fact, with the foresight of the genius, left his own real theory of natural selection open to modification by this acknowledgment. He was indeed forced to do this for he well knew that natural selection did not account for the origin of the variations on which it worked. The effect of use or disuse on the parts of organisms was the only cause of the production of variations that Darwin could consider valid at the time.

Thus true "Darwinism" includes at least a part of Lamarck's theory. A similar position was taken up by some of Darwin's greatest supporters, such as Romanes in England.<sup>1</sup> As Darwin aged he came to believe that natural selection was of less importance as a factor in evolution than he had at first supposed, and so he leaned more and more towards Lamarckism. Other so-called Darwinists, however, did not accept any part of Lamarck's theory, for they considered that natural selection was of universal applicability, and indeed that its universality followed from the very nature of the principle.

The chief advocate of this view was Alfred Russel Wallace, the co-discoverer with Darwin of natural selection. Later a

<sup>1</sup> Romanes defends this position of Darwin in detail in the introduction to Vol. 2 of *Darwin and after Darwin*. Kellogg (1907, p. 264) remarks: "In taking up our brief exposition of Lamarckism, let me say first that only in post-Darwinian years has Lamarckism been put so strongly in contrast with Darwinism as it has. Darwin himself included part of Lamarckism as a minor factor or influence in his explanation of adaptation and species-forming, and Plate, in the recent most notable critical discussion of Darwinism, takes nearly exactly the old ground of Darwin, namely an acceptance of the inheritance in some degree and under some conditions, of acquired characters, and the consequent possibility of a certain amount of Lamarckian orthogenesis, i.e., an orthogenesis due to the inheritance of the results of use, disuse and functional stimuli. It is only neo-Darwinism (of Weismann, Wallace and others) and neo-Lamarckism (of Spencer, Packard and others) that are so radically opposed, so mutually exclusive."

similar position was taken up by Weismann and his school, and by other naturalists such as Ray Lankester and Lloyd Morgan.<sup>1</sup> To these people the theory of natural selection gave an adequate explanation of all organic evolution. This school of thought developed quickly in response to a view which was beginning to grow rapidly, a view which emphasised the Lamarckian aspects of Darwinism and relegated natural selection to a very subordinate place in the scheme of evolutionary causation. Inasmuch as natural selection was Darwin's chief tenet, the new school of Weismann and others became known as that of the neo-Darwinists (a term invented for them by Romanes).<sup>2</sup> Likewise the school which emphasised Lamarckian principles was called neo-Lamarckism.

Neo-Lamarckism was chiefly developed in America by such men as Packard, Cope, Osborn and others. The chief European upholders of the view were Herbert Spencer and Eimer. It is as well to emphasise here that Darwin, as represented by his teachings, occupied a position midway between these two schools.<sup>3</sup> Generally speaking it may be said that the neo-Lamarckians revealed the inadequacy of natural selection as a factor in organic evolution, while the neo-Darwinists (particularly Weismann) showed that there was little, if any, objective evidence for the inheritance of acquired characters. Thus neither school advanced any theory which could be said to replace (or even displace) that of Darwin's idea of natural selection. The views of these various schools are described below.

## 2. ALFRED RUSSEL WALLACE

We have already mentioned A. R. Wallace in connection with Darwin's discovery of natural selection. It has been said that he "out-Darwinised Darwin": in fact, in his book *Darwinism* (1889), he claimed to expound "Pure Darwinism". Although not strictly a neo-Darwinian (for he was contemporary with Darwin) he retained a firm belief in the supreme importance of natural selection in organic evolution until his death. Thus he can be described as being "ultra-Darwinian". Wallace wrote several books on the theory of natural selection. In his *Darwinism* he sets forth

<sup>1</sup> Weismann brought in several subsidiary theories in order to explain away various difficulties of the natural selection theory; the Englishmen Ray Lankester and Lloyd Morgan did not, however, accept many of these theories.

<sup>2</sup> 1895, Vol. 2, p. 12.

<sup>3</sup> A lively controversy ensued between the rival parties: a general idea of the views and position of each of them may be obtained from a debate in the *Contemporary Review* for 1893 and 1894 between Spencer and Weismann.

this theory as enunciated by Darwin and answers many of the objections which he contends caused Darwin to recede from his earlier position in which natural selection was considered to be the real factor in evolution. In the preface to this book Wallace writes: "I thus take up Darwin's earlier position, from which he somewhat receded in the later editions of his works, on account of criticisms and objections which I have endeavoured to show are unsound. Even in rejecting that phase of sexual selection depending on female choice, I insist on the greater efficacy of natural selection. This is pre-eminently the Darwinian doctrine, and I therefore claim for my book the position of being the advocate of pure Darwinism."

Romanes, however, cannot condone this view of the Darwinian theory advocated by Wallace, and in a table given below he puts

Table 1 (1)

*Comparison of Darwin's and of Wallace's Theories of Selection*

<i>Theory of Natural Selection according to Darwin.</i>	<i>Theory of Natural Selection according to Wallace.</i>
Natural selection has been the main means of modification, not excepting the case of man.	Natural selection has been the sole means of modification excepting in the case of man.
(a) Therefore it is a question of evidence whether the Lamarckian factors have operated.	(a) Therefore it is antecedently impossible that the Lamarckian factors can have co-operated.
(b) Neither all species, nor, <i>a fortiori</i> , all specific characters, have been due to natural selection.	(b) Not only all species, but all specific characters, must necessarily have been due to natural selection.
(c) Thus the principle of Utility is not of universal application, even where species are concerned.	(c) Thus the principle of Utility must necessarily be of universal application, where species are concerned.
(d) Thus, also, the suggestion as to sexual selection, or any other supplementary cause of modification, may be entertained; and, as in the case of the Lamarckian factors, it is a question of evidence whether or how far they have co-operated.	(d) Thus, also, the suggestion as to sexual selection, or of any other supplementary cause of modification, must be ruled out; and, as in the case of the Lamarckian factors, their co-operation deemed impossible.
(e) No detriment arises to the theory of natural selection as a theory of the origin of species by entertaining the possibility, or the probability, of supplementary factors.	(e) The possibility—and <i>a fortiori</i> the probability—of any supplementary factors cannot be entertained without serious detriment to the theory of natural selection as a theory of the origin of species.
(f) Cross-sterility in species cannot possibly be due to natural selection.	(f) Cross-sterility in species is probably due to natural selection.

<sup>1</sup> From Romanes, 1895, Vol. 2, p. 6.

forward the theory of natural selection according to both Darwin and Wallace. The differences between the interpretations of natural selection by the two chief co-discoverers of the principle are thus readily seen and appreciated.

In 1871 Darwin published the *Descent of Man and Selection in Relation to Sex*, in which he took his theory to its logical conclusion, and contended that man was descended from an ape-like form. Darwin's theory of natural selection was by this time popular: he seemed to provide scientific proof that evolution had really occurred, natural selection being the causal agency. Now, in this book, he popularized man's descent from the brutes. He had by no means been the first to see a close affinity between man and the apes, but his views became accepted by many people of intelligence, and so the search for the "missing link" began. This link, or lower form, from which man had presumably descended was said by Darwin to be "a hairy quadruped furnished with a tail and pointed ears, probably arboreal in its habits. . . ."<sup>1</sup> The intellectual faculties of man presented a difficulty to Darwin, for, on his theory of natural selection, they too must have evolved from the meagre faculties of animals. He attempted to overcome this stumbling block by assuming that the mind of man differs only in *degree*, not in *kind*, from the "minds of animals".<sup>2</sup> By implication, therefore, man's soul also has evolved from the corresponding vital principle of animals. The whole trend of the argument in this book is obviously directed to showing that man is nothing more than an animal, no doubt highly evolved, but still brutish. Darwin here is, of course, speculating.

It is also on this question of the total origin of man, mentally and physically from animals that Wallace further differs from Darwin. Wallace considers that the evidence of the evolution of man's bodily structure from some form common to man and the anthropoid apes is overwhelming and conclusive. Further, he considers that variation and natural selection have probably brought about this change. Man's body is only a part of him; of more importance as distinguishing him from the lower animals are his moral and intellectual nature. Wallace finds that no attribute of this side of man can be found in any animal in any form. Man's moral perception and various mental faculties are superimposed on his physical nature by an outside agency.

<sup>1</sup> 1871, 1st Ed., p. 889.

<sup>2</sup> 1871, p. 370.

Natural selection can have had no part in developing them. "The special faculties we have been discussing clearly point to the existence in man of something which he has not derived from his animal progenitors—something which we may best refer to as being of a spiritual essence or nature, capable of progressive development under favourable conditions. On the hypothesis of this spiritual nature, superadded to the animal nature of man, we are able to understand much that is otherwise mysterious or unintelligible in regard to him, especially the enormous influence of ideas, principles and beliefs over his whole life and actions."<sup>1</sup>

In the world of animals and plants natural selection is the sole evolutionary factor according to Wallace, but, anticipating objections to his views, he does not admit that this method of evolution necessarily implies that no other cause of ultimate origins can be entertained. In fact, he points out that the development of life by some new power, or cause, other than natural selection, was necessary at three stages, and, further, that the intervention of this cause did not break the continuity of evolution. These stages are (a) the change from inorganic to organic, (b) the change from plant to sensitive or conscious animal, and (c) the change from animal to rational man.

Thus we see that Wallace's views regarding the evolution of man are essentially the same as those of Mivart, although the arguments used by both writers differ. To Mivart, however, the cause bringing about the change from animal to man is the First Cause, or God, who creates each individual human soul, while to Wallace this cause is to be found in "the unseen universe of spirit".

### 3. THEORIES SUPPLEMENTARY TO NATURAL SELECTION

#### (a) *The Theory of Sexual Selection*

Sexual reproduction is a common, but by no means the only, method of reproduction enabling an organism to perpetuate its kind. There are also several types of sexual reproduction, but among the higher organisms at least it implies that there are two kinds of individuals in any one species—male and female. These are differentiated from one another by an essentially physiological distinction, and their concomitant anatomical and morphological accompaniments. By means of these distinctions the essence of

<sup>1</sup>Wallace, 1889, p. 474.

sexual reproduction, i.e., the union of dissimilar sex cells, can be realised. There are, then, both male and female internal and external generative organs, the primary sex organs, which distinguish the sexes. Observation, however, shows us very clearly that other outward characteristics serve to separate the sexes. These characters have nothing whatever to do with the actual sex act, and so they are called the secondary sex characters, possessed by one or other of the sexes in each species.

The important feature of secondary sex characters is that they are developed to a high degree in one sex only. There are many examples of them, such as the large comb of the cock, the beautiful plumage of many male birds, the beard of the man, the antlers or horns of many male animals, the mammae which distinguish female mammals, etc. Plate <sup>1</sup> gives a useful classification of such secondary sex characters.

Sexual dimorphism of this kind has to be accounted for on an evolutionary basis. Darwin, in *The Origin of Species*, recognised that they created a problem for him, and suggested a form of sexual selection which was later developed in his *Descent of Man*. He finds two chief laws regulating the mating of animals, (a) the law of battle and (b) the law of beauty. It is a fact that, during the mating season, many male animals fight among themselves for the "possession" of the female, while the latter remains passive and accepts the victor as a mate. Among many animals in which the law operates the possession of well-developed antlers, horns, or other fighting instruments would be a decided advantage to the possessor. Such instruments are useful to the possessor in the struggle for existence, and hence they can be accounted for by the natural selection of those animals in which they are best developed.

But other secondary sex characters are apparently useless, such as the reduced wings of some male insects, or the combs and wattles of many male birds. Others again can only be described as being harmful to the possessor in the struggle for life. Examples of these are the so-called "exciting" organs, such as the gay, conspicuous and elaborate plumage of some male birds, or their striking colours which if they serve to attract potential mates, also serve to attract enemies. Natural selection cannot account for such characters, and so Darwin described his law of beauty which implies that such secondary sexual characters of the male stimulate the æsthetic feelings of the female, with the result that the female chooses, or selects,

<sup>1</sup> 1903, pp. 107-111.

the male with the best colours, and so on. As Darwin says: "This surprising uniformity in the laws regulating the difference between the sexes in so many and such widely separated classes is intelligible if we admit the action throughout all the higher divisions of the animal kingdom of one common cause, namely sexual selection." Granted that the males chase the females at the time of the mating season then this whole sexual selection theory is built up on the supposition that the female exerts a *choice* on a male because of his greater physical attractiveness due to colour, plumage, odour, patterns, etc. Thus it is necessary to attribute a fairly high degree of æsthetic feeling to many animals which on other grounds would seem to be incapable of such high emotions.

Before sexual selection could intensify secondary sexual characters, the females of successive generations must select for mating only those males which show continuous variations in one direction. If we assume that many animals possess æsthetic feelings we should also assume that these same animals have preferences—some may prefer variations in one direction, some in another, and some may prefer those males which vary but little. The *selecting* power of sexual selection is then cancelled out. Many like objections have been raised against this theory of the evolution of secondary sex characters, so much so that it has been largely discarded.

### (b) *Isolation Theories*

Jenkins' objection to natural selection on the grounds that, due to cross breeding, any favourable variation in a population would be swamped, was widely considered to be valid. Selectionists, who considered that evolution occurred through the inherited accumulation of Darwinian variations, had therefore to find out how this difficulty could be overcome. Moritz Wagner in 1868 put forward a theory of geographical isolation which overcame the difficulty. Later other biologists extended the range of isolation to include in it many biological phenomena as well as mere spatial geographical distribution.

The word isolation explains itself. Generally speaking it means that if, say, a few plants bearing a favourable character become isolated from the parent species in such a way as to prevent cross-breeding with them, then breeding will take place only between plants possessing the character concerned, and, hence, by inheritance the new variation will become fixed, eventually producing a new



species. Obviously, like natural selection, isolation does not get to the root of the problem for it does not explain the origin of the variety. As Kellogg<sup>1</sup> says: "Isolation is a tremendously favouring condition but not a primary cause of species-forming. It tends to help along, to hurry up species disintegration, not to initiate it. It is a biological catalytic agent."

Isolation is accepted by all naturalists as a factor in the perpetuation of variations but there is some difference of opinion as to its relative importance compared with the action of natural selection. On one hand we have Wallace who considered that isolation effected some modification of species not, however, "on account of any effect produced or influence exerted by isolation *per se*, but because it is always and necessarily accompanied by a change of environment, both physical and biological."<sup>2</sup> Hence isolation only aids natural selection by enabling it to do its work more quickly.<sup>3</sup> On the other hand, Romanes, considers that isolation is of far greater importance than natural selection, for he says: "Indeed, I believe, with Mr. Gulick, that in the principle of isolation we have a principle so fundamental and so universal that even the great principle of natural selection lies less deep, and pervades a region of smaller extent."<sup>4</sup> Heredity, variation and isolation rank together as co-equals on which depends the whole theory of organic evolution. There is no doubt at all, so far as isolation prevents inter-breeding between a separated variety of a species with the rest of that species, that it plays an important part in the differentiation of divergent types.

Moritz Wagner first published his view about *The Law of the Migration of Organisms* in a paper read at Munich in 1868, and he stoutly maintained his original views in a series of writings until his death.<sup>5</sup> He assumed that animals possess an innate tendency urging them to migrate into areas where the environment may be less severe than the one in which they were born. The inevitable

<sup>1</sup> 1907, p. 242.

<sup>2</sup> 1889, p. 150.

<sup>3</sup> We may note that Wallace did not accept Jenkins' criticism of natural selection. He contended that the swamping effect of inter-crossing between varieties and parents will not be effective providing that simultaneous variations of individuals occurs. This, he said, is a demonstrable fact. (See Chapter 3, and pp. 142-44, *Darwinism*, 1889.)

<sup>4</sup> 1897, Vol. 3, pp. 1-2.

<sup>5</sup> See Stanford's trans. of *The Darwinian Theory and the Law of the Migration of Organisms*, London, 1872; and *Die Entstehung der Arten durch Raumlliche Sonderung*, 1889 (the Collected Papers) and Bibliography.

result of this must be that states of geographical isolation are set up. Providing that new environmental conditions are encountered in the new situation, then natural selection will contribute to produce new varieties and species. Otherwise, "where there is no migration, that is, where no isolated colony is founded, natural selection cannot take place."<sup>1</sup> Thus Wagner believed that, apart from human action, the only form of isolation was that brought about by the formation of geographical barriers. His theory was based on extensive observations made while travelling as a naturalist in America, Asia and Africa.

In Wagner's time the attention of naturalists was largely centred on the study of individual variations, and the ways and means whereby such variations could be perpetuated by means of natural selection. Hence Wagner's theory was to a great extent overlooked. In 1872 J. T. Gulick,<sup>2</sup> on the basis of an extensive study of some terrestrial mollusks (*Achatinellidae*) of the Sandwich Islands, concluded that for evolution to occur two conditions are necessary, namely, *separation* and *variation*. By *separation* Gulick means any isolation, whether geographical or biological, which prevents cross-breeding. Unlike Wagner, to Gulick separation does not necessarily "imply any external barriers, or even the occupation of separate districts." He supposed that diverging forms of a species possess an inherent tendency so strong that "all that is necessary to secure a divergence of type in the descendants of one stock is to prevent, through a series of generations, their intermingling with each other to any great degree."<sup>3</sup>

In 1887 Gulick presented his views in greater detail in the *Journal of the Linnean Society*. In the first place, Gulick distinguishes between two kinds of evolution (a) monotypic evolution, or transformation of a species without change of its unity of type, and (b) polytypic evolution, or divergent evolution, in which in any transformation of a species different types appear in different sections. Divergent evolution provides us with a real theory of the origin of species by transformation. Gulick considers that neither natural, sexual, or artificial, nor any other kind of selection, can bring about divergent evolution. Natural selection supplies a reason why the less fit (due to early death) are prevented from breeding with the more fit, and so by continual selective breeding

<sup>1</sup> 1872, Engl. trans., by Stanford, p. 59.

<sup>2</sup> *Nature*, 1872 a and *J. Linn. Soc. (Zool.)*, 1872 b.

<sup>3</sup> 1872, b., pp. 498-499.

(exclusive breeding) of the more fit it leads to monotypic evolution—the type, however, remains constant. There are grades of fitness, for different kinds of variations manage to survive. Natural selection cannot account for the divergence of those which propagate successfully. Polytypic evolution is evidently bound up with the kind of breeding which takes place between these varieties. If we can find the cause of the separate generation of these forms, then the evolution of one species into many species will be explained. Gulick considers that this divergent evolution is brought about by separate or segregate breeding of the different kinds of a species. “In other words, Exclusive Breeding of other than average forms cause Monotypic Evolution, and Segregate Breeding causes Divergent or Polytypic Evolution.”<sup>1</sup>

The type of breeding which occurs, therefore, determines the type of evolution, and this in turn will be determined by segregation of forms. By segregation Gulick means isolation. Wagner knew only one type of isolation, viz. geographical, but Gulick describes some eighteen different types, all of which are treated in detail.

The rôle of isolation in evolution is also treated in detail by Romanes<sup>2</sup> who holds very similar views to those of Gulick, and, like the latter, he distinguishes two fundamental types of isolation, (a) discriminate (segregate breeding) and (b) indiscriminate (separate breeding). For these types he coins new words, namely, *homogamy* and *apogamy* respectively. According to Romanes “we may say that if the other two basal principles are given in heredity and variability, the whole theory of organic evolution becomes neither more nor less than a theory of homogamy—that is, a theory of the causes which lead to discriminate isolation, or the breeding of like with like to the exclusion of unlike.”<sup>3</sup> In this way, by isolation of like from unlike forms, Jenkins’ criticism is overcome, but in the process Darwinian natural selection is relegated to a wholly subordinate position.

Romanes is a true Darwinian, but recognises that natural selection cannot be the sole cause of evolution. The recognition of the rôle of isolation enables him to see that there are different forms of evolution and by this recognition many of the difficulties appertaining to the theory of natural selection become

<sup>1</sup> 1887, p. 208.

<sup>2</sup> 1897, Vol. 3.

<sup>3</sup> 1897, Vol. 3, p. 6.

resolved.<sup>1</sup> Although Romanes is so emphatic in his insistence on the overriding importance of isolation, it is necessary to point out that the phenomenon gives rise to a theory of differentiation, while that of natural selection gives rise to a theory of adaptation. Probably few biologists would agree completely with Romanes while still recognising that isolation plays an important rôle in the evolution of species.

The form of homogamy which Romanes considers of most importance in species forming is what he calls "physiological selection."<sup>2</sup> By this is meant the isolation of variants of a species which are fully fertile *inter se* but infertile with the parents, or unlike variants, due to some physiological change in their reproductive systems. A determinate, differential fertility is thus set up among the variations of a species which would of itself tend to segregate them and at the same time ensure their perpetuation. Romanes considers that there is little chance of new forms of species developing unless the other forms of isolation (including that of natural selection) are associated with physiological selection. This theory has been subject to considerable criticism. Perhaps the strongest attack comes from H. Seebohm<sup>3</sup> who points out that the conditions necessary for the operation of physiological isolation would rarely arise because, as he says:

"1. The special variation of the reproductive organs must occur in two individuals, otherwise the possible ancestor of the new species would leave no descendants.

2. It must occur at the same time in both.

3. It must occur at the same place.

4. The two individuals must be of opposite sexes.

5. They must each possess some other variation, or their progeny would not differ from that of the rest of the species.

6. The variation must be the same in both or appear simultaneously in the majority of their children, otherwise it would be swamped by inter-breeding within the physiologically isolated family."<sup>4</sup>

<sup>1</sup> Again, Romanes says: "Hence it is that, while no Darwinian has ever questioned the power of unaided selection to cause *improvement of character in successive generations*, in common now with not a few other Darwinians, I have emphatically denied so much as the abstract possibility of selection alone causing a *divergence of character in two or more simultaneous lines of change*." (Vol. 3, 1897, p. 38.)

<sup>2</sup> 1897, Vol. 3, Chapters 3-5.

<sup>3</sup> 1886.

<sup>4</sup> Romanes was the leading exponent of the theory of physiological selection, but he was not the first to advocate it. He himself points out that Thomas Belt foreshadowed it in his *The Naturalist in Nicaragua*, p. 207. Catchpool enunciated its chief features in 1884 in *Nature*, Vol. 31, p. 4, while Gulick worked it out for

The difficulties raised by Seebohm may appear to be formidable, but modern studies in evolutionary mechanisms have largely rendered them invalid. Fleeming Jenkins' criticism of natural selection still stands today unless the supplementary theory of isolation is brought in, for it is now recognised that all evolutionary divergence involves some kind of isolation. With the growth of genetics new kinds of isolating mechanisms have been discovered all of which tend to overcome the nullifying effects of cross-breeding of variations. Broadly speaking, there are three main types of isolation recognised today, namely geographical, ecological and physiological (including genetical) isolation. We will leave these to be dealt with in a later chapter.

(c) Roux's "*Battle of the Parts*"

In 1881 W. Roux suggested that besides an external struggle for existence between animals and plants there was also an internal one between the parts of an individual. This struggle between organs, tissues and cells was visualised as being created by functional stimuli resulting in a competition for food. By means of this idea Roux was able to give an explanation of the many wonderful inner adaptations, such as arrangements of muscle-fibres in tissues. Roux himself considered that his theory considerably extended the idea and scope of natural selection. He has, however, been drastically criticised by several biologists, such as Plate, who, indeed, considers that the theory is just an extension of Lamarck's theory of the inheritance of acquired characters, for what is it but an account of the effects of use or disuse of various organs, tissues, etc. The theory, however, is important from the historical point of view because, by supplying a scientific explanation of inner adaptations, it takes organic ideas a stage further in their drift towards mechanism.

---

15 years and published his results a year later than Romanes in 1886. (*J. Linn. Soc. Zool.*, 20, pp. 189-274, 1887.) A letter of Gulick's entitled *Diversity of Evolution under One Set of External Conditions* was read at the British Association meeting of 1872, which thus gives the real priority to Gulick. Kellogg (1907, p. 261) also points out that this principle enters into the make-up of Eimer's theory of evolution by means of orthogenesis.

Other supporters of the theory of isolation in evolution at this time include F. W. Hutton (1897, *The Place of Isolation in Evolution*, Nat. Science, Vol. 11, 240-246), and D. S. Jordan (1905, *The Origin of Species through Isolation*, Science, N.S., Vol. 22, 545-562.)

*(d) Organic Selection*

One of Mivart's principal objections to natural selection was that it failed to account for the survival of the initial stages of any incipient useful variation. As an organism develops it shows what is called ontogenetic adaptation, i.e., it is continually adapting itself to its environment, and thereby producing some useful structures. Natural selection would then favour these modifications, but unless fixed in the germ plasma they would not be propagated by heredity. Suppose now that the organism concerned also possesses an innate, or inherited capacity for producing a variation similar to the environmental modification. Taken by itself this innate variation may be too small to be affected by natural selection, but, surely, the combined effects of inherited variations and modifications acting together would be greater than when each acts alone. In this way, owing to the usefulness of an acquired character or modification, individuals possessing an innate capacity for varying in that direction would be favoured by natural selection. Natural selection would then continue to act along this determinate line throughout succeeding generations, until in the end, and through Darwinian accumulation, the innate variation would be so strong as to show itself independently, and thus itself be subjected to the action of natural selection.

This is essentially the theory of organic, or coincident selection proposed almost simultaneously by Lloyd Morgan, J. Mark Baldwin and H. F. Osborn in 1896. The theory overcomes Mivart's difficulty of the non-selection of incipient stages of useful organs or variations, while, at the same time, it accounts for cases of parallel variation. It was proposed after Weismann had given his criticisms of neo-Lamarckism, and while it was still necessary to account for the apparent cases of the inheritance of acquired characters. For it is often claimed that such acquired characters are seemingly inherited because they are coincident in the same individual with an innate adaptive variation. Organic selection is thus a compromise between the pure Darwinian theory of natural selection and Lamarck's of the inheritance of acquired characters. As such it is obviously a useful supplementary theory of evolutionary methods, and it is made use of at the present day, although J. S. Huxley<sup>1</sup> considers that biologists seem to ignore it too much. It

<sup>1</sup> 1942, p. 523.

is as well to remember that organic selection is just a *suggestion*, for little evidence seems to have been produced in its support.

The theory is put very concisely by Morgan in a letter to Baldwin<sup>1</sup> where he says: "My own modest contribution to the further elucidation of the subject is the suggestion (1) that where adaptive variation  $v$  is similar in direction to individual modification  $m$ , the organism has an added chance of survival from the coincidence  $m + v$ ; (2) that where the variation is antagonistic in direction to the modification, there is a diminished chance of survival from the opposition  $m - v$  and hence (3) that coincident variations will be fostered while opposing variations will be eliminated. If this is so, many of the facts adduced by Lamarckism may be interpreted in terms of the survival and gradual establishment of coincident variations by natural selection under the favourable enviroing conditions of somatic modifications."

(e) *Weismannism*

The connection of cytology with evolution was not recognised until some years after Darwin's theory came out. Although Spallanzani in 1786 had discovered the spermatozoa, it was not definitely shown until 1824 by Dumas and Prevost that they were fertilizing elements. The first person to observe the actual process of fertilization was Newport, who, in 1854, saw the spermatozoon enter a frog's egg. In 1875 Hertwig stated that of the two nuclei which fuse in the fertilized egg, one comes from the sperm and the other from the egg itself. Four years later, Schmitz described a similar fusion occurring in plants. The essence of sexual reproduction was thus realised to be the fusion of a male and a female gamete, or nucleus. The resultant cell (or zygote) develops to become an individual which thus has received something from each of its parents.

Apart from this theory of pangenesis, Darwin had contributed but little to the elucidation of the relation between heredity and evolution. Round about 1885, however, Weismann, Hertwig and von Kölliker independently came to the conclusion that the nucleus is the bearer of the hereditary substance. Weismann's theory is the forerunner of modern cytology, although increased proficiency in technique and staining methods has led to profound changes in the modern theory as compared with Weismann's

<sup>1</sup> See Appendix C of Baldwin's *Development and Evolution*, 1902, p. 347.

speculative hypothesis. His theories are set forth in the *Das Keimplasma*<sup>1</sup> and the *Vorträge über Deszendenztheorie*.<sup>2</sup> The account of the theories given here is partly taken from that given in the *Evolution Theory* translated by J. Arthur Thomson and M. R. Thomson.<sup>3</sup>

Weismann considers that the chromatin substance of the nucleus is the substance concerned in heredity. After Nägeli he called the operative part of the nucleus the idioplasm, although by this word Nägeli referred to the cytoplasm rather than to the nucleoplasm. Every cell of a body has a nucleus, hence every cell contains idioplasm. He singles out the hereditary substance of the germ cells as being distinct and of special importance, and so this idioplasm he calls *germplasm*. The hereditary substance in the idioplasm, or germplasm, is represented by the *idants* which in most cases, but not in all, correspond to the visible chromosomes. The idants are made up of *ids* (perhaps identifiable with the chromatic granules often visible in the chromatin, or the chromosomes). The ids in turn contain *determinants* which finally are made up of the ultimate living units, or *biophors*.

The id is a biological unit and it is through the operation of all the ids in a body that that body develops the form peculiar to itself. Each id, therefore, contains within itself the primary constituents of an organism and these may, firstly, be different, or similar, but bearing no relation to the specific parts of the future organism, or secondly, they may all be different, each one then bearing some specific determining relation to some specific part of the future organism. Weismann favoured the second alternative and he called these primary constituents which determined the existence and nature of particular parts of the organism, the *determinants*. The ids of the same species are almost identical. But if one or a few of the determinants become altered the effect would be to produce an animal of the same species but with some part slightly changed, i.e., to produce a variety. The fully developed organism contains many regions which are indeed subject to numberless kinds of variations, hence there must be at least as many determinants as there are such regions in the organism; this also applies to the organism in its ontogenetic or developmental stages. The determinant then is the basis of Weismann's theory of the germ

<sup>1</sup> 1892.

<sup>2</sup> 1902.

<sup>3</sup> 1904.



plasm. By it he attempts to explain how variations are inherited, how freaks develop, how mimics are produced and so on.

In the sense that, by assuming the presence of these determinants in the ids of the germ plasm, it is possible to give explanations of the development of particular parts of organisms, or how variations are produced, we see that they are actually symbols which may or may not represent definite entities. As Weismann says: "Hypothesis begins when we attempt to make creatures of flesh and blood out of these mere symbols, and to say how they are constituted."<sup>1</sup> A determinant as an abstraction is one thing, but a determinant as an actually existing entity is a totally different thing. However, one can be certain that, whatever they are, they are not miniature models or organisms, or of parts of organisms, in Bonnet's preformation sense. Further, Weismann asserts that they cannot be mere material substances; they must be "living parts, vital units", otherwise they would be destroyed by the metabolic activity of the organism in the course of its development. The determinants themselves must be capable of nutrition, growth and reproduction. Here Weismann is in disagreement with some of his modern counterparts, for the gene, the modern hereditary particle, is often thought to be merely a chemical, or even a group in a side-chain of a chemical, which, however, can still reproduce itself. The living ultimate units Weismann calls the *biophors*. In spite of the fact that they are considered to be capable of assimilation, dissimilation, growth and can move, etc., they are still mechanical, for Weismann will not admit of a vitalistic interpretation of life.

The sex cells of the male and female hence contain all the kinds of determinants necessary for the development of an organism. On fertilisation these determinants are brought together in the zygote. As the latter undergoes divisions and goes through the various stages of development until the fully formed organism is produced, these determinants present in the idioplasm sort themselves out to definite regions of the body. They then split up into the contained biophors which give the specific characters to the cells in which they are present by acting on the protoplasm. The cells then give specific form to the part in which they are situated. This sorting out of the ids and the determinants occurs during cell division, for, according to Weismann, no two daughter cells are ever exactly similar to their mother cell. As ontogeny proceeds

<sup>1</sup> *The Evolution Theory*, trans. A. and M. R. Thomson, 1904, p. 368.

the differences between cells become more and more marked, ultimately producing cell groups, or organs, etc.

A criticism advanced against this idea of a continually splitting mass of determinants was that, if it is true, the chromatin of the nucleus (or the idioplasm) would gradually get less and less until ultimately there would be none left. This is contrary to the known fact that the bulk of the chromatin remains relatively constant in adult cells of the organism. Weismann overcame the difficulty merely by assuming that as the *kinds* of determinants get less and less in the dividing nuclei the number of each kind of those remaining increased by division until when "only one kind of determinant is present there is a whole army of determinants of that kind."<sup>1</sup>

There is another difficulty confronting this theory. During the course of development the determinants are continually divided out among different regions of the body of the organism, but the germ cells (the ovum and the sperm) have to contain the complete total of these determinants. How is this brought about? The biophors cannot arise *de novo*. Before any germ cell can be produced all the relevant determinants must be present. Weismann got over this difficulty by postulating that the germ plasma of the germ cells is continuous from generation to generation. After fertilisation the zygote divides into two identical cells, one of these gives rise ultimately to the body of the organism concerned, while the other gives rise to the germ cells contained in that organism. This theory of the continuity of the germ plasma was stated by Weismann first in 1885. By this theory the somatic cells became recognised to be distinctly separated off from the germ cells. The somatic cells live and die but the germ cells are potentially immortal, and hence they alone can transmit hereditary qualities to the future generations. The germ cells alone maintain the species and keep it going.

This distinction of germ cells and somatic cells is the greatest contribution which Weismann made to biology. It has been elaborated by the modern geneticists into the genetical selectionist viewpoint.

The chief evolutionary theories in vogue at this time were Darwin's theory of natural selection, Lamarck's theory of the inheritance of acquired characters and the theory of orthogenesis. Weismann's theory of the germ plasma, which postulates such a radical distinction between the idioplasm of the body cells and

<sup>1</sup> *The Evolution Theory*, trans. A. and M. R. Thomson, 1904, p. 379.

germ plasm of the germ cells, was really an attack on the Lamarckian position. According to Lamarck the environment affects the body of an organism causing a slight change, this change is then passed on from the body cells to the germ cells, which transmit it to the next generation. According to Weismann, this is impossible, for the body cells and germ cells are distinct.

So Weismann became the great opponent of Lamarckism, and in fact he brought forward many objections to that theory. He pointed out that no one had brought forward any *direct* proof of the inheritance of acquired characters. The *indirect* evidence for the theory was also found to be unsatisfactory. Herbert Spencer first brought forward the Lamarckian argument of co-adaptation. This means that a modification of one part of the body of an organism in order to be of any adaptive use implies the simultaneous modification of many other parts all working under the action of natural selection. In fact, Spencer argued that these co-adaptive changes must extend not only to other organs but in many cases to the tissues of the animals concerned. Consider the evolution of an antelope into a giraffe. As the hind quarters gradually changed to become the hind quarters of the giraffe there must have been corresponding changes in the fore-quarters. Each of these changes alone would require a very large number of secondary changes in the body of the incipient giraffe. As Romanes<sup>1</sup> says: "Yet, if we exclude the Lamarckian interpretation which gives an intelligible *cause* of co-ordination we are required to suppose that such a happy concurrence of innumerable independent variations must have occurred by mere accident—and this on innumerable different occasions in the bodies of as many successive ancestors of the existing species." If at any time during the evolution of the giraffe co-ordination of all these parts failed then natural selection would have weeded them out. To believe that evolution, which seems to be so ordered a natural process, occurs in this way makes very great demands on our credulity.

Weismann admitted this as a difficulty but he was not prepared to accept wholeheartedly the assumption that a simultaneous variation in all parts was necessary. Later he pointed out that the phenomena of co-adaptation occurs in worker bees and ants which do not reproduce and so could not pass on their modifications. Further, in arthropods, which moult regularly, co-adaptations are found in "passively functioning parts". Moultings are often

<sup>1</sup> See Romanes, 1897, Vol. 2, pp. 64-65.

accompanied by changes, new parts are developed, or existing parts are further developed with each succeeding moult. But these changes take place beneath the hard chitinous outward shells from cells which belong to the true skin of the animal. It is impossible then for such changes to have been brought about by the inheritance of use because they are not used till after the moult. They can only have been formed in the ancestor of these animals by sudden changes before use. Thus Weismann says: "We therefore reject—and are compelled to reject—the Lamarckian principle, not only on the ground that it cannot be proved correct, but also because the phenomena to explain which it is used, occur also under circumstances which absolutely exclude any possibility of the co-operation of this principle."<sup>1</sup> Weismann, however, is merely assuming that the new cells formed beneath the chitinous skin of the animal have no use in that stage.

To counteract any experiments which may seem to show that an external stimulus has caused a bodily change which was inherited Weismann brought in the idea of *parallel induction*. In this idea the stimulus affects the germ plasm at the same time as it affects the body or soma. At least in multicellular organisms, inherited variations can only arise (1) through changes in the germ plasm in response to internal stimuli or the like, or (2) through recombinations of the inherited factors brought about at the time of fertilisation. That does not mean to say that the body cannot pass on a change to the germ plasm. These different points of view can be seen readily from the following diagrams (figure 1).

Evolution is thought to take place through the accumulation of minute variations occurring again and again, and which are of some definite advantage to the organism, and hence become naturally selected. Excluding the effects of hybridization, to Weismann evolution could only take place through the accumulation of variations induced in the germ plasm. To explain how this was brought about he extended the idea of natural selection of large adaptive characters to the germ plasm and so produced his theory of *germinal selection*. Previously Roux had extended the theory of natural selection to include in its scope the internal organs of organisms. Now Weismann extends Roux's struggle of the parts to include invisible living units, or biophors. The theory of germinal selection also gave an explanation of the way by which the so-called useless organs were enabled to disappear.

<sup>1</sup> 1904, Vol. 2, p. 99.

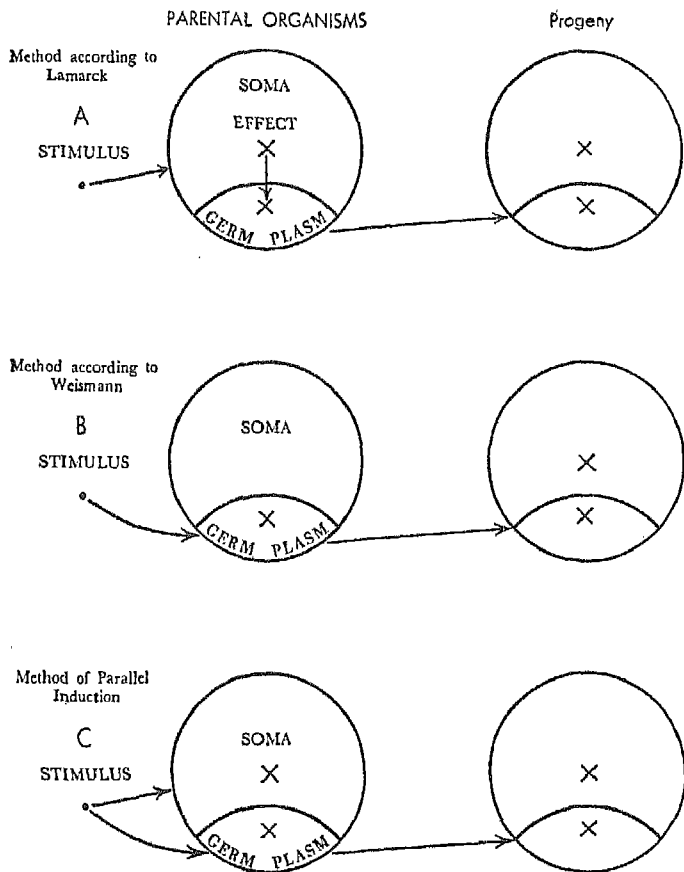


Figure 1. Legend

*Diagrams illustrating the different interpretations of inherited environmental effects*

The organism is represented by a circle divided into two parts; the larger part represents the soma or body, while the smaller part represents the germ plasm; an appropriate environmental stimulus (represented by a black dot) acts on the organism and produces its effect (X) in the organism. The circles on the left hand side represent the parental organism, while those on the right hand side represent their progeny. In *A*, the method of inheritance according to Lamarck, the stimulus produces an effect (X) in the soma of the parent, which passes it on to the germ plasm and thence to the progeny. In *B*, the method of inheritance according to Weismann, the stimulus acts on the germ plasm directly, which then passes it on to the progeny. In *C*, the method of inheritance according to the idea of parallel induction, the stimulus acts on both germ plasm and soma together, while the germ plasm passes it on to the progeny.

The germ plasm, according to Weismann, is composed of particles, determinants and biophors. These are living and hence require nourishment for their growth and reproduction. Weismann assumes that there must be a state of equilibrium between these particles, and any upset in this state would lead to an outward change in the structure of the organism. If some determinants obtain more nourishment than others, this will lead to their better and quicker growth. Those that are slow-growing and receive less nourishment will remain weaker, and when transmitted to an animal, will produce a weaker part, or organ. If inequalities in the nourishment of the determinants persist for a long time they will gradually lead to an effect which will be observable. The organs produced by these determinants will then gradually become of less and less use. The opposite also applies. Those determinants receiving the most food will gradually go from strength to strength with a corresponding effect on the organs they give rise to. According to the available food supply, as Weismann says: "The determinants are in constant motion, here ascending, there descending, and it is in fluctuation of the equilibrium of the determinants system that I see the roots of all hereditary variations."<sup>1</sup> There is thus a struggle for existence between the determinants; the concept of natural selection is thereby extended to the germ plasm, and there becomes directly the cause of variations. Once variations are induced in the germ plasm they will, of course, be transmitted by heredity.

We see then that Weismann has really two chief theories, first a theory of heredity and second the extension of this by means of germinal selection into a theory of evolution. Thus Weismann was an ultra-selectionist, and all his theories were designed either to answer objections to natural selection, or to counteract the growing influence of the neo-Lamarckians. Weismann was, in fact, the foremost neo-Darwinian. In some ways the theory of germinal selection, while professedly an extension of natural selection, is also a theory of orthogenesis, for by the selection of determinants variations are set along a definite and predetermined course of development. As Delage and Goldschmidt<sup>2</sup> comment on it: "It is one of the logical among orthogenetic theories, for it accounts, at least hypothetically (the determinants being hypothetical), for definite variations. It is a causal and

<sup>1</sup> 1904, Vol. 1, p. 118.

<sup>2</sup> 1912, pp. 155-6.

mechanical interpretation of orthogenesis." And again Weismann's theory of germinal selection is an extension of Roux's theory of the 'battle of the parts'. Just as Roux's idea was bound up with the development of an organ, or part of an organ, by use or disuse, by just so much also does Weismannism become related to Lamarckism, in spite of the author's extreme bias towards Darwinism. His theories are, of course, purely speculative and abstract, but by means of them Weismann was able to explain many problems confronting evolutionary biologists.

While Weismann's ideas have now been abandoned there is one important thing that they did: they drew attention to the germ cells as containing the mechanism whereby hereditary qualities are passed on from generation to generation. Weismann thus forced biologists to concentrate their energies on the study of the nucleus and so, in this way, he opened up the path for the future connection of cytology with genetics, which subjects are now the pillars of the modern selectionist theory of evolution. J. Arthur Thomson<sup>1</sup> tells us that these theories of Weismann stimulated research "more than any other biological idea except that of natural selection."

#### 4. THEORIES REPLACING NATURAL SELECTION

##### (a) *The New Lamarckism*

In Chapter 4 an account of the chief work of Lamarck was given, and emphasis was laid on the fact that he was the first biologist to put forward a complete theory of organic evolution. He was, of course, preceded by a few outstanding naturalists like Buffon and Erasmus Darwin, who acknowledged some form of organic evolution, but could not quite decide how it came about. For various reasons Lamarck's views were shelved, but with the coming of Charles Darwin's theory of natural selection attention was focused on them once more, for Darwin, and his truer supporters like Romanes, recognised that, although natural selection operates universally, it does not work exclusively. Later still, after the death of Darwin, the two ideas of evolutionary causation, while not basically contradictory, became opposed to each other by two different schools of thought, namely the neo-Darwinians and the neo-Lamarckians. An exaggerated Darwinism gave rise to a resurrection of Lamarckism, so that the latter indeed, towards the

<sup>1</sup> 1899, p. 12.

end of the nineteenth century, was put forward as a theory superseding that of natural selection, for it offers an alternative method of species-forming independent of selection.

We have now to consider this new Lamarckism, and hence it will be as well to summarise Lamarck's chief teachings in this regard as follows:—

1. His first aim was to create a system of philosophical zoology based on the belief that species *were mutable*.

2. He discerned a principle of perfection inherent in animals.

3. He asserted that the environment exerts an influence on the state of perfectibility of animals with the result that change, i.e., evolution, occurs as follows:—

- (a) This influence on animals brings about certain reactions in them. From these reactions certain requirements result.

- (b) A change of requirements brings about a change of action leading to the establishment of habits.

- (c) As the performance of habits involves the use of certain organs their frequent use will develop them at the expense of those which are used less. Use leads to development or modification; disuse leads to deterioration.

- (d) A persistent modification produced by continued use under the stimulus of the environment, that is, a functionally induced modification, is passed on by heredity to succeeding generations providing the modification occurs on both sexes.

- (e) Finally, a time factor intervenes between use and appearance of the modification.

If we accept the doctrine of evolution, and exclude the mystical side, then only one of these tenets of Lamarckian doctrine is controversial, and that is, the one concerned with the inheritance of acquired characters. The whole theory indeed depends on this: if responses of the individual to the environment are inherited Lamarckism becomes the simplest and most widely applicable theory of the evolution of species. For it accounts at once for the origin and survival of variations. It is a much more complete and satisfactory theory than that of natural selection, which is a theory of survival only. On the other hand, if acquired characters are not inherited, the whole theory collapses. It is of some importance to note that there has probably been at all times a conviction among ordinary folk that behaviour of a present generation influences the succeeding generation. And surely this conviction has a good effect on human society in general.



Thus the experimental study of Lamarckism became the study of the inheritance of acquired characters, i.e., of what is called the Lamarckian principle. Those neo-Darwinists who believed in the exclusive action of natural selection had no use for this principle, but even such a staunch neo-Darwinist as Weismann had to have recourse at least once to the principle. The mere theoretical denial of Lamarckism by the neo-Darwinians was insufficient to stem the interest in it which was aroused by the formulation of the evolution principle by Darwin. It was necessary to show that it was invalid and unnecessary. Weismann attempted to do this by means of his various subsidiary theories of the germ plasm and parallel induction. By the complete separation of the germ plasm from the soma, such as was postulated by Weismann, the vehicle for the transmission of functionally acquired characters was rendered immobile; while by means of parallel induction Weismann was able to explain any case of such inheritance without appeal to the Lamarckian principle. Weismann's theories, however, were just as speculative, if not more so, than those of Lamarck, and so neo-Lamarckism became a legitimate theory of organic evolution.

Lamarckism indeed is a theory which has been very elaborately developed, and it is impossible here in the space at our disposal to do more than indicate its scope. Many Lamarckians, such as Eimer and Cope, were also orthogeneticists.<sup>1</sup> But for convenience of arrangement their views will be considered separately under the heading of "Orthogenesis".

It was inevitable that, as Lamarckism stands for the environment as the determining agent acting on the organism, then new researches should be directed into new untried channels. The early Darwinians accepted the fact of inheritance but assumed that new variations were passed on to succeeding generations. Not so the Lamarckians for with them the study of evolutionary biology meant the study of the environment, development and heredity. Lamarck, by postulating the inheritance of acquired characters, initiated an era of experimental biology among his followers, for it was necessary to determine experimentally what characters were acquired and how they were inherited.<sup>2</sup>

<sup>1</sup> Indeed, Lamarck himself believed in straight line evolution, or orthogenesis, but to this conception he added the action of the environment and the factor of use and disuse.

<sup>2</sup> An account of some of the more important Lamarckian experiments is given in a later chapter.

The experimentalist, seeking to prove the Lamarckian principle, faces many difficulties such as that of definition of what is meant by an acquired character (and there are conflicting opinions about this), or difficulties of experimentation, or again difficulties of interpretation of experimental results for often such results can be expressed in terms of either natural selection or of Lamarckism. Indeed it is this last-mentioned difficulty which causes many biologists to waver in their choice between Darwinism and Lamarckism. In short, *a priori* methods of reasoning are deeply ingrained in all of us, but it is when such methods are applied to problems of practical biology that our interpretations become nebulous and instead of arriving at a scientific conclusion we do but make a *choice* of possible solutions of the problems involved. It is here that the *a posteriori* method comes to our aid. Many adaptations of organisms are explicable by the application of either the Darwinian or the Lamarckian theory. But to say a thing is true because it can be explained by such and such a theory is a travesty of the laws of reasoning. It may be true, or it may not. We can only arrive at a further approximation to the truth by attacking the problem backwards, and so finding out if sensible experience supports our theory, i.e., by endeavouring to find out if that which our theory postulates does actually occur. In the realms of pure metaphysics the *a priori* method is a sound way of arriving at such conclusions, but in the realms of empirical science its value is doubtful because it is so easily abused.

On *a priori* grounds then Lamarckism is an ideal and acceptable causal theory of evolution, and as such, it demands our attention, but on *a posteriori* grounds it lacks confirmation for there are few known examples illustrating the truth of the Lamarckian principle.<sup>1</sup> It is here of course that the time factor enters in, for nature works slowly, and merely because our experiments show that the effects of a use or disuse stimulus are not inherited does not mean that under natural conditions a similar stimulus applied to generations of organisms over a long period would not produce an inherited effect. In the final analysis then we are still left with a choice between rival theories. Lamarckism can be neither proved nor disproved. This does not matter to the work-a-day practical biologist, for he finds himself in a similar position with regard to the theory of organic evolution in general. Theoretically he believes

<sup>1</sup> This may also be said of Darwinism; both theories have got hold of something fundamental and they are logically unassailable.

that species are mutable but, for the purposes of his day by day experimental work, he must assume that the species he is dealing with will not change overnight as it were, i.e., that it is immutable during his experimental work. This does not prevent him from believing in organic evolution in the general case.

There are several outstanding writers of the Darwinian and neo-Darwinian era who advocated Lamarckian ideas, or extended his theories. One of the first of these was Herbert Spencer, who had done so much to prepare the way for the reception of *The Origin of Species*, and who, in his *Principles of Biology* (1864) and other writings, gave a philosophical status to the then new theory of evolution. Spencer in fact substituted the phrase "survival of the fittest" for the term "natural selection". He was never, however, really a selectionist because from the beginning his views were Lamarckian, and he laid great stress on the inheritance of acquired characters. He should be considered the first of the neo-Lamarckians. In the last section of his *Factors of Organic Evolution*<sup>1</sup> by applying the *a priori* method Spencer arrives at the conclusion that in the evolution of organisms as their organisation becomes progressively more and more complex the Lamarckian factor comes more and more into play, and the Darwinian factor recedes into the background until finally in the case of man, in whom the operation of natural selection is limited, this factor has become the chief one.

The principal neo-Lamarckians, however, were the American original workers like Hyatt, Cope, Osborn and others. It was probably only in the United States of America that a definite School of neo-Lamarckism existed. Many of these were palæontologists. In 1886, A. Hyatt began to publish the results of his researches on fossil cephalopods which, as regards their theoretical import, were purely Lamarckian. In the same year Cope published his *Origin of Genera*,<sup>2</sup> and in this and later books he emphasised the over-riding importance of the environment in evolution. Along with Hyatt he claims to have demonstrated this when he says: "In other words, these publications constitute the first essays in systematic evolution that appeared. By the discovery of the palæontologic succession of modifications of the articulations of the vertebrate, and especially mammalian, skeleton, I first furnished an actual

<sup>1</sup> 1887, comprising reprinted papers from the *Nineteenth Century* of 1886, p. 74.

<sup>2</sup> This was first published in *Proc. Philadelphia Nat. Soc.*, 1868, and separately in 1869; see also Chapter 2 in *Origin of the Fittest*, 1887.

demonstration of the reality of the Lamarckian factor of use, or motion, friction, impact and strain, as an efficient cause of evolution."<sup>1</sup>

Since the time of these early neo-Lamarckians there has been a steady stream of supporters, too many of them to be mentioned here in this short outline. Suffice to say that an excellent historical summary of neo-Lamarckism is given by A. S. Packard<sup>2</sup> in his biography of Lamarck. The reader is referred to this book. Packard was an ardent Lamarckian, and he sums up the viewpoint and the position of the more or less modern theory admirably in the following passages which we take the liberty of quoting. "Neo-Lamarckism gathers up and makes use of the factors both of the St. Hilaire and Lamarckian schools, as containing the more fundamental causes of variation, and adds those of geographical isolation or segregation (Wagner and Gulick), the effects of gravity, the effects of currents of air and of water, of fixed or sedentary as opposed to active modes of life, the results of strains and impacts (Ryder, Cope and Osborn), the principle of change of function as inducing the formation of new structures (Dohrn), the effects of parasitism, commensalism, and of symbiosis—in short, the biological environment; together with geological extinction, natural and sexual selection, and hybridity." And again, "It is to be observed that the Neo-Lamarckian in relying mainly on these factors does not overlook the value of natural selection as a guiding principle, and which began to act as soon as the world became stocked with the initial forms of life, but he simply seeks to assign this principle to its proper position in the hierarchy of factors." And finally, "Were the dogma of natural selection to become universally accepted, further progress would cease, and biology would tend to relapse into a state of atrophy and degeneration. On the other hand a revival of Lamarckism in its modern form, and in a critical and doubting attitude towards natural selection as an efficient cause, will keep alive discussion and investigation, and especially, if resort be had to experimentation, will carry up to a higher plane the status of philosophical biology."<sup>3</sup>

We can finish this account of neo-Lamarckism by referring to a staunch upholder of the doctrine, and one whose writings have been sadly neglected. Samuel Butler was a philosopher who

<sup>1</sup> Cope, 1886, p. 9.

<sup>2</sup> 1901.

<sup>3</sup> Packard is here quoting from his own paper of 1894.

looked at evolution as an outsider. Probably because of this he could see the failings of the doctrine and its various theories. Butler wrote several books on evolution<sup>1</sup> in which he opposed Darwinism and supported the theories of Buffon and Lamarck. Indeed he considered that Darwin deliberately ignored the works of these earlier men. Butler thought that natural selection was of little value as a factor in organic evolution, and its influence was mainly negative. He resolutely opposed the rule of chance which is inherent in early Darwinian theory, and he is perhaps best known for his mnemonic theory in which development is explained by using memory as a bridge between embryo and parent. The egg contains in mnemonic form all the accumulated experiences, instincts and tendencies of the parent and past ancestors.

Butler's memory theory, like the theories of Hering and Semon, overcomes many biological difficulties. For example, as the embryo possesses potentially all the past experiences of its ancestors, then the successive stages of ontogeny are merely the unfolding of memory stages one after the other in logical order. The mnemonic theory thus gives an explanation of why ontogeny recapitulates phylogeny. Such a theory also gives an explanation of heredity which as Radl points out "is merely an exercise in memory." An individual is constantly repeating his daily actions. They tend to become habits. Perfection results from use and the response to the environment is to develop new parts or modes of making new parts. Thus experience accumulates, and leaves a memory which is made use of by succeeding generations. Such a theory of memory is, of course, thoroughly Lamarckian.

#### (b) *Orthogenesis*

In 1884, Carl von Nägeli published a new rationalistic interpretation of evolution called the *Mechanico-physiological Theory of Evolution*<sup>2</sup> in which he put forward his views that evolution proceeds because of a persistent advance towards perfection from a simpler to a more complex organism. Natural selection to him was only a secondary causal factor in evolution producing an adaptive state in the organism, the urge to perfectibility was the primary causal agency at work. Nägeli pictured life as constantly arising from dead matter due to the interaction of the

<sup>1</sup> See Bibliography.

<sup>2</sup> Leipzig, 1884.

physical and chemical forces. Once simple cells had been produced in this way, their structure determined the further processes of growth, reproduction, variation, etc., which thus followed on mechanically.

The products of Nägeli's abiogenesis are not really cells as we know them because these are well differentiated structures. Such cells are far too complex to arise *de novo*. Nägeli thought that by spontaneous generation living things arose as drops of homogeneous stuff which he called *Mizellen*. Two kinds of protoplasm are produced from them—(a) the idioplasm which possesses the qualities of the organism concerned and which is contained in a nutritive plasma, and (b) the stereoplasm. The idioplasm impresses its form on the stereoplasm which is different in different parts of the body. Due to internal causes consequent upon its structure this idioplasm changes constantly from generation to generation, with the result that the structure becomes more and more differentiated and complex. In this way new forms arise and evolution occurs. Thus by evolution Nägeli means a progression towards perfection brought about by indefinable internal urges. Co-existent with the striving towards structural perfection there is a striving towards perfection of adaptation. This is because the new forms that arise as results of the internal causes have to live in, and be adapted to, the external world which affects them. Nägeli's views thus have a touch of vitalism about them; indeed he was accused of mysticism by the Darwinians, although he himself considered his theory to be purely mechanical.

Nägeli's views were not founded on observational facts; they are purely intellectual in origin, and, while there is a touch of vitalism about them, they are really anti-teleological, for his "perfecting principle" represents the "law of inertia in the organic realm", as Morgan puts it. His view of a driving force propelling organisms along a predetermined evolutionary path is only one among several such orthogenetic ideas advocated about this time. As Korschinsky<sup>1</sup> says: "In order to explain the origin of higher types out of lower it is necessary to assume a special tendency towards progress in the organism". The Lamarckian theory is also an orthogenetic one, but it is ever so much more than this. The various theories of orthogenesis can be distinguished according to the special factor which they visualise as producing the orthogenetic variations. Many orthogenetic results are also

<sup>1</sup> 1899, p. 273.

explicable in terms of natural selection, and the name orthoselection has been given to this type, which is usually excluded from the ordinary orthogenetic theories, for it is one of the chief merits of orthogenesis that it serves to give an explanation to forms of evolution which the Darwinians are unable to account for. Indeed, one of the real difficulties of Darwinian theory is to explain the persistence of incipient stages of incipient organs before the useful stage is reached; or, again, Darwinism fails to explain the determinate development along fixed lines not advantageous, and it also fails to account for the fantastic over-development of organs far beyond any degree of usefulness, such as the huge size of the cretaceous reptiles, or the over elaborate plumage of some male birds.

Orthogenesis, however, does give a coherent explanation of these difficult cases. The palæontologist has found many examples of evolutionary series in the stratified rocks which seem to indicate that evolution has proceeded along certain paths, or along certain fixed lines. We find examples of such series in the fossil records of the horse, the elephant, the ammonites, and the titanotheres. In such cases the variations as they occur do not seem to be due to chance in a Darwinian sense; they do not conform to the variation curve of the law of error. Evolution in such cases is not due to chance; orthogenetic evolution, in fact, is like the unrolling of a tremendously long stair carpet, which, as it gradually unrolls, displays the ever-changing but pre-determined pattern woven into it.

The point arises what is it that determines the pattern, what is it that determines the direction which the evolutionary path takes? Generally speaking, there are two broad opinions as to this. Some orthogenetic theories follow the ideas of Nägeli and postulate an internal urge which operates over and above the physico-chemical forces at work in organisms. Other orthogenetic theories find a propelling force in either the internal or external environment or organism. This is considered to be a material factor which acts with the physico-chemical forces of the organism moulding it in a certain direction. The action of this factor then is essentially physiological, and this is the strength of the orthogenetic view of evolutionary causation for, as Cunningham<sup>1</sup> tells us, there is evidence that physiological change precedes morphological. Some biologists, however, such as Wells and Huxley, would disagree with this division of orthogenetic theories into two chief types. According to these writers straight line evolution is deter-

<sup>1</sup> In the Preface to his translation of Eimer's *Organic Evolution*.

mined only by an inward directive force.<sup>1</sup> Such a view may not be correct, for Eimer, one of the foremost orthogeneticists, wrote: "I find the actual causes of orthogenesis to lie in the effects of external influences, such as climate or nutrition, or the constitution of a given organism."<sup>2</sup>

The essential point of all orthogenetic theories is that their advocates see the operation of law in the organic world. There is a unity in organic nature which does not permit of the operation of indiscriminate forces. Sentiments like this have been expressed by all the leading orthogeneticists such as Eimer, while Osborn writes: "As in the domain of inorganic nature, so in the domain of organic nature *fortuity is wanting*."<sup>3</sup> The most complete modern exposition of the subject adopts this attitude deliberately, for Berg calls his excellent book *Nomogenesis or Evolution determined by Law*, and throughout it he contrasts his ideas and the ideas of other orthogeneticists with those of the Darwinians who are forced by the postulates of Darwinism to believe in evolution by means of the natural selection of indiscriminate fortuitous variations. Orthogeneticists do not deny the work of natural selection, but they describe it as a conservative, not a changing force. Berg realises that straight line, or determinate, evolution approaches the teleological conceptions of Aristotle, and he does not shrink from its implications. He counters adverse criticisms from this standpoint by declaring that contemporary physics shows us that the phenomena of the physical world are likewise subject to the rule of law which works on them along a definite line.

As already implied, there have been many supporters of the orthogenetic idea. Besides those already mentioned some others are E. Koken (1902), W. Scott (1894), C. D. Whitman (1919) and J. C. Willis (1922).

Without going into any further detail of the views of individual workers, it may be sufficient for our purpose to conclude this section by quoting some of Berg's conclusions on the merits of orthogenesis. These conclusions, which were arrived at in a scientific manner, are important for they epitomise a body of informed opinion which is anti-selectionist.<sup>4</sup>

<sup>1</sup> 1934, Vol. 3.

<sup>2</sup> Quoted from Delage and Goldschmidt, 1912, p. 299.

<sup>3</sup> 1909, p. 225.

<sup>4</sup> The reader who wishes to examine the details of orthogenetic theories should consult Cunningham's translation of Eimer's *Organic Evolution* (1890), or E. D. Cope's *The Origin of the Fittest* (1887), where a theory of archæsthetism is developed.



Berg<sup>1</sup> writes : "The Discussion we have followed through chapters 2 and 3 leads us to recognise the following laws:

1. *Higher characters or their rudiments appear in Lower groups very much earlier than they are manifested in full development in organisms occupying a higher position in the system.*

It may be inferred from this that evolution is to a considerable degree an unfolding of pre-existing rudiments. But, as will be seen from the sequel, it would be incorrect to maintain that evolution is preformation pure and simple.

2. *The successive manifestations of new characters are governed by law. In the process of evolution there is no place for chance: new characters appear where they should appear. Evolution is nomogenesis, or development determined by law.*

Just as ontogeny pursues its destined course prescribed by law (the antecedent stage preparing and predetermining the subsequent one), so is evolution accomplished by means of law.

3. *Therefore evolution follows a determined direction.* There is no chaotic variation, as was assumed by Darwin.

4. *Some characters owe their development to internal (autonomic) causes inherent in the very nature of the organism, and independent of any effects of the environment.*

These are fundamental, the most essential characters which determine the very plan of structure of a given group. It is perfectly obvious that the ontogenetic process, for instance, is effected by these intrinsic causes alone.

5. *The laws of development of the organic world are the same both in ontogeny and phylogeny.* Thereby may be explained the much talked of 'recapitulation of phylogeny by ontogeny'."

### (c) Heterogenesis

The arrival of the theory of heterogenesis, or the mutation theory of evolution, brings us to the end of the Formulative Period in our history of the Idea of Evolution. It is essentially a bridging theory between the ideas of this period and those of the Modern

<sup>1</sup> This is taken from Berg's *Nomogenesis*, translated by J. N. Rostovtsov, 1926, pp. 154-156.

This is a theory of orthogenesis in which the primary factor influencing the organism is consciousness (really sensation). A synopsis of the views of both of these writers is given by Kellogg (1907). And also Berg's *Nomogenesis* (Rostovtsov's trans., 1926.)

Synthetic Period. Although, at first, the mutation theory was probably thought to replace Darwinian ideas, with the reformulation of Mendel's principles after 1901, it later became recognised that some mutations could be identified with some small variations. If mutations are the outward signs of inward slight changes in the germ plasm then heterogenesis can be made to agree with Darwinian ideas. For this agreement a satisfactory theory of heredity is first of all necessary, and until this was provided mutations, or saltations as they were originally called, if they contributed at all to the evolution of organisms, could only be imagined as doing so in a manner contrary to the ideas of Darwin. It was Mendel who first supplied the beginnings of a theory of heredity which, as it developed, was to be used to reconcile the mutation theory with Darwinism, giving rise to what we may call the Modern Synthetic Theory of Evolution.

The Darwinian theory of evolution depends on the cumulative selection and inheritance of very small variations in the direction of usefulness. So-called Darwinian variations are indeed shown by organisms. The advantageous ones among these were said to furnish the process of evolution with its raw material, but with the rise of the mutation theory many biologists were not prepared to accept this Darwinian contention. Discontinuous variations, or sports, have long been known to biologists. Darwin described some of them, such as the Ancon sheep, or the Paraguay cattle, in his *Plants and Animals under Domestication*. Many of these sports breed true, and so it was inevitable that they should be made use of in evolutionary theories, although Darwin considered that, because of their relatively rare appearance in nature, they did not provide adequate material on which selection could work in an evolutionary sense. The earlier of the theories of heterogenesis were incomplete, and could not be regarded as substitutionary theories for that of natural selection until de Vries brought forward his views.<sup>1</sup>

De Vries distinguished clearly between the various types of variations. Chiefly we have those ordinary ever-present fluctuations, and such variations as "happen to arise". It is these latter types that de Vries calls *mutations*. Such mutations may be large or small; the essential point about them is that their appearance

<sup>1</sup> In this section it is necessary to deal in outline with the original theory of mutation, i.e. with heterogenesis proper as it was contrasted with Darwinism. The modern theory, of course, will be dealt with later.

cannot be foretold; they occur fortuitously, suddenly and abruptly. Such mutations, which have been studied in horticulture, de Vries identifies with the variations which Darwin considered were used for evolutionary changes. In this way he seeks to show that his theory is in "the fullest harmony with the great principle laid down by Darwin." Few biologists would agree with this, however, for the essence of Darwinism is that by the natural selection of minute variations evolution is a continuous process. Whereas, by definition, de Vriesian mutations are abrupt changes and so are discontinuous. Besides, Darwin did not distinguish between the various kinds of variations. He assumed that all variations were inherited.<sup>1</sup>

Leibniz' tag "*natura non facit saltus*" is only true to a certain extent for, as Berg reminds us, it is equally correct to say "*natura facit saltus*". According to Berg: "Every kind of progress is achieved by bounds. *Rhythm*, manifested in the physical as well as in the ideal world, is nothing more than an exhibition of the law of intermittent development. The birth or death of individuals, species, ideas is a catastrophic process. The manifestation of every class of these phenomena is preceded by a long latent period of development, which follows certain laws, and then suddenly culminates in a bound, *saltus*, by which the group emerges into the light, is distributed over the earth's surface, and wins for itself 'a place in the sun'."<sup>2</sup> Berg here gives a full definition of mutations, and he is expressing opinions which cover both the biological and geological fields, for the idea of saltatory evolution is by no means confined to biologists.

The first person who considered discontinuous variations (or saltatory variations as he called them) to be of some value in organic evolution seems to have been A. von Kölliker, who, in 1864, brought forward a theory of heterogenesis. Kölliker, who was an anti-Darwinist, considered that saltatory variations arose from internal (physico-chemical) causes in accordance with a general law of evolution. In 1869 W. Waagen put forward a mutation theory, but here the mutations were changes only in a geological sense in that they are observable only in the transition period of time between one geological stratum and another. Such mutations are independent of external conditions for similar

<sup>1</sup> See *Darwin and Modern Science*, ed. by A. C. Seward, 1909, Chapter by De Vries, pp. 71 and 74, and footnote on page 71 by A. C. Seward.

<sup>2</sup> 1926, pp. 387-388.

ones appear under different geological conditions. Hence they are not to be confused with de Vriesian mutations.

In his *Genesis of Species*, Mivart (1871) discusses some of the views of the naturalists (such as Darwin, Wallace, Huxley, Naudin, Godron, Owen, Murphy and others) who have recounted the sudden origination of new forms from old ones. He contends that: "Arguments may yet be advanced in favour of the view that new species have from time to time manifested themselves with suddenness, and by modifications appearing at once, the species remaining stable in the intervals of such modifications: by stable being meant that their variations only extend for a certain degree in various directions, like oscillations in a stable equilibrium."<sup>1</sup> Later in 1876 Baer and in 1877 Dall supported the idea of saltatory evolution. While in 1885 Danilevsky gave some account of what he called sudden spontaneous variations. Cope<sup>2</sup> recognised that some generic changes may have been rapid, others slow: change of generic type he considered had taken place more rapidly than change of specific type. In 1889 Korschinsky brought forward his theory of heterogenesis in which heterogeneous variations were considered to be the raw material of evolutionary change.<sup>3</sup>

William Bateson did not consider the doctrine of descent to be proven, but he accepted it as a postulate on account of the difficulty of accepting any alternative doctrine, such as that of separate creation, which he regarded as absurd. Assuming evolution to occur, then he found that the two principal causal theories, i.e., those of Lamarck and Darwin, face a great difficulty which he expresses as follows: "According to both theories, specific diversity of form is consequent upon diversity of environment, diversity of environment is thus the ultimate measure of diversity of specific form. Here then we meet the difficulty that diverse environments often shade into each other insensibly and form a continuous series, whereas the specific forms of life which are subject to them on the whole form a discontinuous series."<sup>4</sup> In his famous *Materials for the Study of Variation* (1894) Bateson did not propagate any definite theory of evolution by means of mutations, but he certainly focused the attention of biologists on to this question of discontinuous variations in organisms. This book is in fact a collection of

<sup>1</sup> 1871, p. 97.

<sup>2</sup> 1887, pp. 78-79 and 83.

<sup>3</sup> We have already dealt with Korschinsky's criticisms of Darwinism in Chapter 5.

<sup>4</sup> 1894, p. 5.

all such mutations that Bateson could find. He discovered that discontinuous variations are so common in nature that "it suggests in brief that the *Discontinuity of Species results from the Discontinuity of Variations*."<sup>1</sup> Hence his conclusion is that the problems of evolution and of species can only be attacked through the study of variation.

Thus by the end of the nineteenth century the idea of heterogenesis was quite well known and acceptable to biologists. It only needed experimental evidence to complete it; this was provided by Hugo de Vries who published his *Mutation Theory* in 1901 after a long and careful series of investigations.<sup>2</sup>

We have already mentioned the distinction de Vries made between the different kinds of variations. Those which are concerned in evolution, called de Vriesian mutations, arise suddenly at a jump from the parent organism. Thus they correspond to what were originally called saltations, or saltatory variations. A new variety, or a new species, is produced at once. Ordinary variations, the Darwinian, or fluctuating variations of Bateson, are produced by the action of the environment and will remain constant so long as selection is maintained. But as soon as this selection ceases the fluctuating variation reverts back to its ancestral type. On the other hand the mutation, or sport, is produced by some change in the germ plasma; it is permanent, and hence may be expected to have an effect on the evolution of the species. Changes in the germ plasma which give rise to these mutations bear no relation to the conditions of the external environment. The change, in fact, is due to something inherent in the organism, and may occur in any, or all, directions. Those changes which are not beneficial will of course be naturally selected; those which are, will survive. In this way new species arise from old ones. In this way evolution proceeds. The process of evolution is thus seen to be due to internal causes. The action of the environment is like that of a sieve, it acts arbitrarily by selecting those mutations that chance to be adaptive in a particular setting. As already mentioned, de Vries did not set his theory in opposition to that of Darwin, but from the very state of biological science at the time it was inevitable that the two theories should be contrasted by other naturalists.

De Vries began his experimental work in 1886 but he did not publish his results until 1901. His observations led him to the conclusion that within a Linnean species there were many varieties

<sup>1</sup> 1894, p. 568.

<sup>2</sup> English trans., 1910.

which may be only slightly different from each other, but which breed true to their varietal characteristics. He called such "little species" by the name of *elementary species*. He then began to investigate the production of elementary species in nature. Eventually he found a plant called *Oenothera Lamarckiana* (the Evening Primrose) which produced a number of new species, or mutants, regularly every year. *Oenothera Lamarckiana* is supposed to be of American origin, and is cultivated in Europe. The plant chosen for investigation by de Vries was found growing wild in a potato field near Hilversum. In de Vries own words: "This stately plant showed the long-sought peculiarity of producing a number of new species every year. Some of them were observed directly on the field, either as stems or as rosettes. The latter could be transplanted into my garden for further investigation, and the stem yielded seeds to be sown under like control. Others were too weak to live a sufficiently long time in the field. They were discovered by sowing seed from indifferent plants of the wild locality in the garden. A third and last method of getting still more new species from the original strain was the repetition of the sowing process, by saving and sowing the seeds which ripened on the introduced plants. These various methods have led to the discovery of over a dozen new types never previously observed or described."<sup>1</sup>

By growing the Evening Primrose in controlled garden cultures for seven generations de Vries found 874 mutations out of 54,343 plants produced. These mutations were of seven kinds some of which were produced only once, or a few times, while others appeared in every generation. Each mutation was given a name as follows:—

<i>gigas</i>	(giant) which appeared in one generation only.
<i>albida</i>	(pale-leaved) which appeared in four generations with a total of 56 individuals.
<i>oblonga</i>	(oblong-leaved) which appeared in five generations with a total of 350 individuals.
<i>rubrinervis</i>	(red-veined) which appeared in four generations with a total of 32 individuals
<i>nanella</i>	(dwarf) which appeared in seven generations with a total of 158 individuals.
<i>lata</i>	which appeared in six generations with a total of 229 individuals.
<i>scintillans</i>	which appeared in three generations with a total of 8 individuals.

<sup>1</sup> 1905, ed. by D. T. MacDougal, p. 525.

Many other mutations have arisen from this species on other occasions; the essential point is that de Vries found many of these mutations were true elementary species and bred absolutely constant to type. As a result of his extensive investigations on *Oenothera Lamarckiana* de Vries was able to formulate several laws governing the appearance of mutations some of which are given below:—<sup>1</sup>

1. New elementary species appear suddenly and attain full constancy at once independently of external conditions.
2. The same new species are produced in a large number of individuals.
3. Mutability is fundamentally different from fluctuating variability for they cannot be grouped around a mean. The mutations themselves vary, however, around their own mean, and this mean is simply the type of the new elementary species.
4. The mutations take place in all directions. Some are adaptive others not, the former will survive, the latter will not. Some are larger, some smaller, some vigorous, some weak, and so on.

Later it became obvious that *Oenothera Lamarckiana* was a hybrid which owed its peculiar breeding behaviour to an unusual (if not unique) state of the chromosomes. The mutation theory, however, is still valid, for later investigators found that non-hybrid varieties of plants and animals could produce mutations. One of the earliest and most important supporters was T. H. Morgan who later became one of the foremost students of heredity of the times.

De Vries next set out to apply his observations of the breeding behaviour of *Oenothera Lamarckiana* to the theory of descent with modifications in general. As the de Vriesian mutations are elementary species then natural selection acts between species and not between mere varieties or individuals of the same species. The mutation theory represents a decided advance in evolutionary speculations for the following reasons:—Darwin emphasised the importance of the action of natural selection on variations which have once arisen. De Vries drew attention to the importance of mutations in evolution while at the same time his views linked up with those of Weismann by his postulation that the mutation concerned arose spontaneously due to changes in the germ plasm. In this manner also de Vries took his stand against the Lamarckian viewpoint.

<sup>1</sup> Adapted from de Vries, 1905, pp. 558-575.

De Vries further claimed that his experimental work on *Oenothera* opened up a new experimental field for biological investigators—an aspect of biology which he considered the pure Darwinian theory to discourage. As he says: “To my mind the real value of the discovery of the mutability of the Evening Primrose lies in its usefulness as a guide for further work.”<sup>1</sup> He considered that mutations must be of universal occurrence, and of the two alternatives, whether mutability is a regularly occurring or a periodic phenomenon, he tended to favour the latter view. The assumption that species mutate periodically in an historical sense helps us to explain many facts of nature. For instance, at any one time we should expect to find some species in a state of mutability, others in a state of immutability, which is seemingly the case. It also helps us to understand the existence of such a polymorphic genus as *Viola* which now shows a period of relative constancy compared with a past period of great fluctuation when the present elementary forms of this genus were produced. Above all, this idea serves to show how the principles of relative stability of species agrees with the idea of organic evolution of species. To avoid error here it is perhaps better to quote de Vries’ own words. He says: “Many facts plead in favour of the constancy of species. This principle has always been recognised by systematists. Temporarily the current form of the theory of natural selection has assumed the species to be inconstant, ever-changing and continuously being improved and adapted to the requirements of the life-conditions. The followers of the theory of descent believed that this conclusion was unavoidable, and were induced to deny the manifest fact that species are constant entities. The mutation theory gives a clue to the final combination of the two contending ideas. Reducing the changeability of the species to distinct and probably short periods, it at once explains how the stability of species perfectly agrees with the principle of descent through modification.”<sup>2</sup>

After the careful work of de Vries the theory of heterogenesis soon became popular, for it was soon recognised that he had supplied evidence that at least some new species arise by means other than the selection of minute variations. Evolution by means of mutations is one type of evolutionary change. As we have already pointed out, once it became recognised that mutations could be small changes as well as large ones, the mutation theory developed into the chief

<sup>1</sup> 1905, p. 686.

<sup>2</sup> 1905, p. 694.



modern theory of evolution. Today a mutation can be defined as any inherited change in the germ plasm no matter how it is caused. De Vries brings to a close the Period of Formulation of the Idea of Evolution by directly showing the value of actual experimentation in the production of new species. Thus by 1901 the concept of evolution was well established, but evolutionary mechanisms were subjects of keen controversy, as indeed they still are. The final stage for the Modern Period was set, that is the application of speculative theories to the phenomena of heredity. Since the time of Darwin, heredity and the concept of the germ plasm had figured largely in evolutionary literature; it was all pure speculation. But it was speculation leading to the idea of particulate inheritance, and so, when Mendel's particulate theory of statistical heredity was re-discovered in 1901, the way was cleared for a truer synthesis of evolutionary ideas in terms of heredity founded on some basis of mathematics. A further stimulus was given in 1903 when Sutton first suggested a cytological explanation of Mendelian phenomena by showing that the behaviour of the chromosomes in cell division and during the production of the gametes fulfilled Mendel's requirements of segregation. From this time onwards evolutionary theory bounded ahead. An account of these developments form the chief subject matter of the next period in this historical survey, i.e., of the Modern Synthetic Period in Evolution.

## PART II

### CYTOGENETICS AND THE MODERN CAUSAL THEORIES OF ORGANIC EVOLUTION.



## CHAPTER 7

### THE MODERN PERIOD FROM 1901 :

#### (A) THE TURNING POINT IN EVOLUTIONARY THEORY

##### 1. INTRODUCTION

THE Darwinian period was the time during which the idea of evolution became firmly established; whether or not one believed in Lamarckism or Darwinism, one accepted the idea of evolution by descent. Thus the principle of evolution was formulated while that of special creation was largely discarded. It is only through the study of heredity that the closest affinity, that of genetic relationship, can be expressed. So it was natural and logical for the chief exponents of evolution during the period of formulation of the evolution idea to insist on the importance of heredity to a study of evolution. Lamarck, by his theory of the inheritance of acquired characters, and Darwin, by his insistence on the inheritability of the favoured characters of the organisms, both recognised that heredity was the vehicle of evolutionary change. When this important point was fully realised the Period of Formulation came to an end. Before any real further advance could be made in the study of evolution it was necessary to understand the mechanism of heredity.

It is noteworthy that both Darwin and Lamarck never attempted any experimental work on heredity. They observed and interpreted, but they never seem to have experimented, observed and interpreted. Thus their theories could never attain to true scientific eminence comparable to that of the great physical theories. The experimental side of evolutionary investigations began with Mendel who first unravelled the mysteries of the mechanism of heredity. Mendelism, by itself, however, could never account for real change in the organism for Mendelian statements are only interpretations, in terms of probabilities, of the possible combinations of known characters of an organism that may or may not occur. Changes, or mutations, occur spontaneously and such have never yet been predicted. The introduction of Mendelism, however, enabled

evolutionists to tackle their problems synthetically, for it enabled them to investigate the problems of the causes of evolution in a new experimental light. Thus the Modern Period may be called the Synthetic Period in the History of Evolution.

## 2. GENETICS

### (a) *The Advent of Mendelism*

Mendelism is essentially a theory of heredity, but, as we have said already, heredity is the vehicle of evolutionary change, and so, to understand evolutionary causation, an understanding of the mechanism of heredity is first of all necessary.<sup>1</sup> The story of Mendel is very well known, but in any historical account of evolution, the corner stone of biological theory known as Mendelism must be given a prominent place. Gregor Mendel became an Augustinian monk of the monastery called the *Königskloster* in Brunn. He devoted much of his spare time to experimental work in breeding plants. Some of his results were published in the journal of the local Natural History Society<sup>2</sup> in 1865-6. For some unaccountable reason, or reasons, these scientific papers, destined to become classics, were scarcely even mentioned by Mendel's contemporaries until they were re-discovered in 1900 by Tschermak, Correns and de Vries who, working independently, had arrived at conclusions similar to Mendel's.<sup>3</sup> Mendel knew of the work of the early plant hybridizers such as Kolreuter and Gärtner, but what is more important, he realised why, although these workers had produced many hybrids, none of them had been able to put forward a theory of heredity. Mendel was able to do this because he analysed his results statistically generation by generation. In the following quotation the three pre-requisites for such an analysis are clearly recognised. "Those who survey the work done in this department (i.e., plant hybridizing) will arrive at the conviction that among all the numerous experiments made, not one has been carried out to such an extent and in such a way as to make it possible to determine the number of different forms under which

<sup>1</sup> Resurrected Mendelism was by no means the first theory of heredity to be advanced.

<sup>2</sup> Mendel, 1865 and 1866.

<sup>3</sup> A trans. of Mendel's Papers reprinted from the *J. Roy. Hort. Soc.* is given by W. Bateson in *Mendel's Principles of Heredity*, 1909, pp. 318-368. Bateson refers to the Paper on *Experiments in Plant Fertilisation* as a "model of lucidity and expository skill" (p. 7).

the offspring of hybrids appear, or to arrange these forms with certainty according to their separate generations, or definitely to ascertain their statistical relations.”<sup>1</sup> Thus Mendel owes his success to his technical methods which enabled him to interpret his results scientifically.

At the outset of his work he recognised that the material chosen for experimental work must be such as to reduce to a minimum the chances of any errors which might vitiate the results.

So he chose the species *Pisum sativum*, the garden pea. Mendel differed from most of his predecessors in this field by confining his attention, not to the plants as a whole, but to certain single pairs of contrasted characteristics, or characters, of the plants as they are called. We are so accustomed nowadays to treat of heredity in terms of single, or only a few, characters of the organism that it is often overlooked how important is this reversal of method first brought about by Mendel. C. H. Waddington<sup>2</sup> puts this very forcibly when he says: “The fundamental step in the understanding of heredity depended on a bold piece of abstract thinking.” The pairs of characters chosen by Mendel were as follows:—

- (a) Forms of seeds which may be either round or wrinkled.
- (b) Colour of cotyledons which may be either yellow or green.
- (c) Colour of seed coat which may be either greyish-brown or white.
- (d) Form of pod which may be either inflated or deeply shrunken between the seeds.
- (e) Colour of unripe pod which may be either green or bright yellow.
- (f) Position of flowers on flower stalk which may be evenly distributed or hunched at the apex.
- (g) Height of plant whether tall or dwarf.

Mendel bred the plants showing these characters until he was satisfied that they were pure, i.e., that a tall plant, for instance, gave rise to nothing else but tall plants when bred with itself or its like, and so on.

When Mendel crossed a pure-breeding tall plant with a pure-breeding dwarf plant, the hybrids of the subsequent or  $F_1$  generation

<sup>1</sup> All quotations from Mendel given here are taken from the translation in W. Bateson's book mentioned above. This one occurs on page 318.

<sup>2</sup> 1939, p. 29.

were all found to be tall. A similar behaviour was found in all the seven pairs of contrasting characters chosen for crossing; in each case the hybrids resembled one or other of the parent forms. Mendel said that those parental characters which appeared in the hybrids were *dominant*, while those which disappeared were said to be *recessive*.<sup>1</sup> This result is unaffected no matter which parent form is used for pollen or which as seed-bearing. When the hybrids of the first generation were crossed among themselves Mendel found that no transitional forms were produced but plants with dominant and recessive characters were produced always in the proportion of 3 dominant to every 1 recessive.<sup>2</sup> Mendel notes that the plants showing the dominant character have a "double significance," i.e., they may possess the character as a pure one, or as a hybrid one. This can only be tested by breeding further to obtain the F<sup>3</sup> generation. It is then seen that those plants with the recessive character, one-third of the total, breed true; while, of those plants with the dominant character, two-thirds of the total, one third breeds true and produces plants with the dominant character and two-thirds give a 3:1 ratio of dominant and recessive characters again just as the hybrids of the first generation. The three to one ratio thus resolves itself into a modified 1:2:1 ratio. Mendel carried his investigations through to several generations. If we represent the dominant character by *A*, the recessive one by *a*, and the hybrid by *Aa*, then these results can be summed up as follows:—<sup>3</sup>

Generation				Ratio		
	<i>A</i>	<i>Aa</i>	<i>a</i>	<i>A</i> :	<i>Aa</i> :	<i>a</i>
1.	1	2	1	1 :	2 :	1
2.	6	4	6	3 :	2 :	3
3.	28	8	28	7 :	2 :	7
4.	120	16	120	15 :	2 :	15
5.	496	32	496	31 :	2 :	31
<i>n</i>				2 <sup>n</sup> -1 :	2 :	2 <sup>n</sup> -1

<sup>1</sup> The dominant characters are put first in the list of contrasting characters given above.

<sup>2</sup> The actual ratios were as follows:

- (a) Form of seed .. .. 2.96 round - 1 wrinkled.
- (b) Colour of cotyledon .. 3.01 yellow : 1 green.
- (c) Colour of seed coat .. 3.15 greyish-brown : 1 white.
- (d) Form of pods .. .. 2.95 inflated : 1 shrunk.
- (e) Colour of unripe pods .. 2.82 green : 1 yellow.
- (f) Position of flowers .. 3.14 axial : 1 terminal.
- (g) Length of stem .. .. 2.84 long : 1 short.

<sup>3</sup> From Bateson's trans. of Mendel's Paper, p. 332.

Mendel next proceeded to consider the contrasting pairs taken in couples and threes at a time, and he expresses the results as follows:—<sup>1</sup> "The results of the previously described experiments led to further experiments, the results of which appear fitted to afford some conclusions as regards the composition of the egg and pollen cells of hybrids. An important clue is afforded in *Pisum* by the circumstance that among the progeny of the hybrids constant forms appear, and that this occurs, too, in respect to all combinations of the associated characters. So far as experience goes, we find it in every case confirmed that constant progeny can only be formed when the egg cells and the fertilising pollen are of like character, so that both are provided with the material for creating quite similar individuals, as in the case with the normal fertilisation of pure species. We must therefore regard it as certain that exactly similar factors must be at work also in the production of the constant forms in the hybrid plants. Since the various constant forms are produced in *one* plant, or even in *one* flower of a plant, the conclusion appears logical that in the ovaries of the hybrids there are formed as many sorts of egg cells, and in the anthers as many sorts of pollen cells, as there are possible constant combination forms, and that these egg and pollen cells agree in their internal composition with those of the separate forms.

"In point of fact, it is possible to demonstrate theoretically that this hypothesis would fully suffice to account for the development of the hybrids in the separate generations; if we might at the same time assume that the various kinds of egg and pollen cells were formed in the hybrids on the average in equal numbers." In further experiments this "theory is confirmed that *the pure hybrids form egg and pollen cells which, in their constitution, represent in equal numbers all constant forms which result from the combination of characters united in fertilisation.*" (p. 343)

By a similar method of reasoning with every point of his results Mendel was led to the assumptions which are at the basis of his theory. He postulated:—

1. The presence of factors, now called genes (which represent characters in the actual plants), in the egg and pollen cells.
2. That in the first filial or  $F_1$  generation different kinds of egg and pollen cells are produced in the hybrid in equal numbers.

<sup>1</sup> Bateson remarks here that these two paragraphs "contain the essence of the Mendelian principles of heredity"; hence they are given in full. See pages 338 and 339.



That is, in the hybrid during the formation of the egg or pollen cells a segregation of factors occurs. This is known as the *law of segregation of factors*. Hence the sex cells will contain only one factor of a pair. This law puts forward the essential feature of Mendelian theory.

3. That the factors of different characters assort themselves independently in the hybrid. This is known as the *law of independent assortment* which has been modified considerably as the science of genetics developed.

4. That in fertilization the egg and pollen cells carrying the independently assorted factors unite at random according to the mathematical laws of chance. This is known as the *law of chance recombination*.

Such is the essence of Mendel's original paper. At first sight it might not appear to be epoch-making, but in actual fact all modern genetics, or theory of heredity, is ultimately based on his assumptions and laws derived from the behaviour of his hybrids. Modern genetics is Mendelism plus modifications, extensions and amplifications to suit special behaviours which our increased knowledge of the constitution of the sex cells has brought to light. *Mendelian inheritance is particulate*, and this feature cannot be too strongly emphasised, whether the factors interact among themselves to produce the characters of the organism or not. Some biologists maintain that particulate inheritance is merely a phase of Mendelian heredity.<sup>1</sup>

#### (b) *The Cytological Explanation of Mendelism*

Referring to the methods of Mendelian enquiry Bateson says:—  
“By this method we reach reality and concrete fact among phenomena that had become almost proverbial for their irregularity. The keys to the problems of genetics and, as we confidently believe, to that of Species also, lies in the recognition of the character-units, or factors, as we often call them.”<sup>2</sup> From Mendelism developed the science of genetics as a direct consequence of Mendel's postulates. Genetics, then, as Bateson further points out, is concerned with the behaviour and nature of the factors which are concerned

<sup>1</sup> To make the theory rather clearer than the historical account given above, a simple explanation based on Mendel's laws is given in modern terminology in the Appendix.

<sup>2</sup> 1909, p. 54.

in heredity. We are not giving a History of Genetics here but only an account of the science sufficient to enable us to trace the chief developments of evolutionary thought, because from this time onwards evolutionary theory and genetics are closely interwoven. The first extension of Mendelian theory occurred in the years 1901 to 1904 when it became more or less established that the behaviour of the chromosomes in cell division, and in the production of the gametes, or sex cells, resembled closely the postulated behaviour of the Mendelian factors. Almost immediately then genetics and cytology became inextricably linked as cytogenetics, and it is due to the application of cytogenetics to evolutionary theory that we owe much of the modern work in evolution.<sup>1</sup>

In the few decades previous to the rediscovery of Mendelism, the study of the cell, or cytology, had made great headway. The cell theory of Schleiden and Schwann had indeed stimulated research in this direction. The first definite declaration of the reality of cell division seems to have been made by Virchow<sup>2</sup> in 1855. In the 1870's Hertwig and later Fol working on animals and Strasburger on plants<sup>3</sup> showed that fertilisation consisted in the union of a nucleus derived from the male parent with one derived from the female parent. From this demonstration in 1884 both Hertwig and Strasburger were able to infer the far-reaching conclusion that it is the nucleus of the cell which bears the physical basis of heredity. In 1885 Weismann put forward his germ plasm theory in which the point is stressed that it is the germ plasm only which transmits the characters of the parents to their offspring. During the same period the behaviour of the cell during cell division became known. As Wilson<sup>4</sup> points out, many workers actually contributed to this discovery. It was found that in cell division, or *mitosis*, as it is called, the nucleus becomes resolved into threads which shorten and thicken to become the chromosomes. Each chromosome splits into two longitudinal and identical halves. The halves then separate and move to opposite points or poles of the nucleus where identical daughter nuclei are re-constituted. Finally van Beneden (1884) showed that the "chromosomes of the offspring are derived in equal numbers from the

<sup>1</sup> A detailed account of the history of the discovery of the cytological basis of Mendelian phenomena is given by Wilson (1928, 3rd Ed., Introduction, chapter 12 and other chapters).

<sup>2</sup> 1855, p. 23.

<sup>3</sup> Hertwig, 1875, 1877, 1878; Fol, 1877, 1879; and Strasburger, 1877 and 1884.

<sup>4</sup> 1928, p. 14.

nuclei of the two conjugating germ cells and hence equally from the two parents.”<sup>1</sup>

It was seen from this discovery of van Beneden that in each act of fertilisation the gametic number of chromosomes became doubled, yet the adult organism always contains the same number, that of twice the gametic number. Obviously, therefore, at some stage in the life history of the organism a reduction in the number of chromosomes must be effected. Weismann indeed had deduced this from theoretical reasons.<sup>2</sup> It took many researches, however, to demonstrate the process of this reduction, or *meiosis*, as it is called, and the time at which it occurs. Generally speaking, meiosis takes place in the germ plasm and leads directly to the formation of the gametes. The most exact definition of meiosis is that given by C. D. Darlington<sup>3</sup> as follows:—“We may now define meiosis by its superficial phenomena as *the occurrence of two divisions of a nucleus accompanied by one division of its chromosomes*. It results in the production of four nuclei, each of which has half the number of chromosomes of the mother-nucleus, provided that their distribution has been regular.”

Henking in 1891 suggested that, prior to meiosis, a conjugation of pairs of chromosomes was brought about and that the actual reduction consisted in the separation of the members of each pair to different nuclei. In the next year Rückert<sup>4</sup> contended that the members of each pair of chromosomes were derived from different parents. In 1902 Boveri,<sup>5</sup> in a classic paper on experimental embryology, stated that “Normal development is dependent upon a particular combination of chromosomes; and this can only mean that the *individual chromosomes must possess different qualities*”.

The cytological stage was now set for the linking-up of cytology with Mendelism, for Mendel had postulated the presence of single genetical factors in the gametes, but pairs of them in the zygote (i.e., the product of fusion of two sex cells). Thus after the re-discovery of Mendelism it was very soon realised that the chromosomes and their behaviour provided a perfect mechanical basis for the transmission of Mendelian factors. This was done, first pointed out by Montgomery in 1901, then by Sutton in 1902-3, by de Vries in 1903, and by Boveri in 1904.

<sup>1</sup> Wilson, 1928, p. 14.

<sup>2</sup> 1887, p. 360.

<sup>3</sup> 1937, p. 86.

<sup>4</sup> 1892, a and b.

<sup>5</sup> 1902, p. 75.

*(c) Pure Line Theory*

In the Darwinian epoch it was thought that continued selection could gradually change a race in any desired direction. It was the custom in those days to select a variation and breed from it in the hope of establishing a new strain. The idea underlying this practice, however, was that variations were all of a similar nature. Little account was taken of the fact that variations may be due to (a) the environment, and (b) the genotypic constitution of the plant. This distinction between the two types of variations was first resolved experimentally by Johannsen, who, in 1903, brought forward the theory of pure lines, which made a distinct advance in our knowledge of the effectiveness of selection. Johannsen worked with the bean plant the flowers of which are self-fertilized. Hence variations in such plants are not due to crossing and segregation of factors, at least in the normal course of events. Nevertheless in populations of the plant, a great deal of variation was observed in a given environment, and selection among these produced an effect, either increasing or decreasing the average weight of the bean seeds. But when the lightest and the heaviest beans from each separate plant were sown and the seeds resulting from them collected, it was found that the beans from the same plant had the same average weight. In other words the weight of the beans from a single plant varied about a mean and selection of beans from this plant was then ineffective.

From his experiments Johannsen concluded that in self-fertilized plants there are no hereditary variations on which selection can work. Each plant is homozygous. Subsequent plants obtained from such a plant are genetically pure, and he called the group so obtained a *pure line*. In the field a population of plants will consist of a mixture of pure lines which may be different genetically, and so selection may be effective. Johannsen was thus able to distinguish clearly between the two kinds of variations, (a) phenotypic variations due to the action of the environment which are not inherited, and (b) genotypic variations caused by differences in the hereditary constitution of the organism. Selection is only of use when it acts on genotypic variations, for then it isolates the factors responsible for the phenotypic characters selected. Its action, however, is merely a sorting out of what is already there. Selection in any case does not create anything new.

In populations of cross pollinated plants selection may be effective up to a time at which the population becomes resolved into a number of pure lines; selection after this point is reached is ineffective, for selection by itself produces nothing new. Mendel first showed that if we start with a hybrid  $Aa$ , then after  $n$  generations of self-pollination the numbers of pure breeding ( $AA$  and  $aa$ ) organisms present in the population can be written as:—

$$AA = \frac{2^n - 1}{2^{n+1}}; \quad Aa = \frac{1}{2^n}; \quad aa = \frac{2^n - 1}{2^{n+1}}.$$

This means that, starting with a heterozygous, or hybrid organism, by continued inbreeding the resultant population would become homozygous but not homogeneous, for it would consist of different pure lines; the number of heterozygotes, or hybrids, in it would be negligible. Informative results have been obtained by mathematical analysis of this kind by carrying out various combinations of crossings and selection by various workers,<sup>1</sup> notable among them being Jennings,<sup>2</sup> Robbins,<sup>3</sup> Wright<sup>4</sup> and Fisher.<sup>5</sup>

### 3. CHROMOSOMES AS AIDS IN SPECIES DETERMINATION

At first the early Mendelians were prone to imagine that the whole chromosomes were the visible expressions of the segregating Mendelian factors. This was natural enough at the time when only relatively few genetical investigations had been undertaken. But, as the number of researches multiplied, it was soon found that the chromosomes, although they may be the material basis of heredity, could not be the factors themselves, because the number of chromosomes in any one organism is relatively small, while the number of characters, the inheritance of which was controlled by factors, was relatively large.

It was found, however, that investigations concerning the number of somatic chromosomes<sup>6</sup> and their gross structure and size could be useful in helping to resolve certain systematic problems

<sup>1</sup> Other investigators who have worked on pure lines and obtained rather similar results to Johannsen's include Zeleny and Mattoon (1915), Ewing (1916), Ackert (1916), Lashley (1916), Castle (1919), Banta (1921).

<sup>2</sup> 1916, a and b; 1917.

<sup>3</sup> 1918.

<sup>4</sup> 1921, a and b; 1930.

<sup>5</sup> 1930.

<sup>6</sup> That is the chromosomes of the body cells as distinct from the meiotic chromosomes, or those of the germ plasma and gametes.

or problems of species determination which have, of course, a bearing on evolutionary problems. We have now to consider the phenomenon known as polyploidy.

Normally each type or variety of plant or animal has a constant number of chromosomes. In many plants (and some animals) the whole complement of chromosomes can be seen to fall into two sets, one set being contributed by one parental gamete, and the other set by the other gamete. If, for example, there are 20 chromosomes in each cell, then at meiosis there will be 10 bivalents, or pairs, of chromosomes. Such an organism is said to be *diploid* (or  $2n$ ). The gametes of each diploid organism will then be *haploid* (or  $n$ ). In many other organisms, particularly plants, there are seen to be three, four, six, or more sets of haploid chromosomes. At meiosis these chromosomes assemble in groups of 3, 4, 6, etc., forming trivalents, quadrivalents, hexavalents, etc. Such plants are said to be triploids, tetraploids, hexaploids, etc., and the whole series is called a polyploid series because the numbers of chromosomes in each member of the series forms a multiple of a basic (or  $x$ ) number of chromosomes. As examples, the species of *Chrysanthemum* have somatic chromosome numbers of 18, 36, 54, 72, and 90, here  $x=9$ ;<sup>1</sup> species of *Solanum* have been found with numbers of 24, 36, 48, 60, 72, 108, 120, and 144, here  $x=12$ ;<sup>2</sup> The chromosome numbers in species of *Potentilla* range from diploid to 16—ploid with  $x=7$  as the basic number.<sup>3</sup> There are very many other examples.

Sometimes a relation is shown between the systematic subdivisions of a genus and the chromosomes. For example, the wheats of the genus *Triticum* fall into three natural groups, and each group has its own basic number of chromosomes as follows:— (a) the *einkorn* group with a basic number of 7, (b) the *emmer* group with a basic number of 14, and (c) the *spelta* group with 21 as the basic chromosome number.<sup>4</sup>

Generally speaking a mere doubling of the chromosome number of a plant does not have much effect on its appearance, for the balance between the chromosomes remains undisturbed, qualitatively they are unchanged. Often an increase in size or vigour is noted. Other numerical chromosomal irregularities, however,

<sup>1</sup> Tahara, 1921.

<sup>2</sup> Jorgensen, 1928; Jorgensen and Crane, 1927; Vilmorin and Simonet, 1927 and 1928.

<sup>3</sup> Shimotomai, 1930, and Müntzing, 1931.

<sup>4</sup> Watkins, 1930.

can arise in plants. Due to several causes, plants may possess one or a few chromosomes more or less than the normal or the polyploid number. Thus we can have plants with  $2n-2$ ,  $2n-1$ ,  $2n+1$ ,  $2n+2$ ,  $4n-1$ ,  $4n+1$ , etc. Such plants are spoken of as *polysomes* or *aneuploids*. Obviously, here the normal balance of the chromosomes is upset. A good example of aneuploids is seen in a whole series of them found in *Datura stramonium* by Blakeslee and Belling.<sup>1</sup> In this plant the haploid number of chromosomes is 12. Thus there are twelve possible  $12+1$  forms in each of which a different chromosome would be triplicated in the plant. All of these were obtained, and, furthermore, the extra chromosome altered the expression of the characters of the plants, chiefly the form of the fruit. Hence each of the twelve aneuploids could be given a name.

An upset of the balance of the chromosome complement has an effect on meiosis during the formation of the gametes which in its turn affects the inheritance of characters. Thus, as in *Datura*, the chromosome number of the plant may play a part in the origination of new varieties. It will be necessary to return to the question of polyploidy and evolution in the next chapter.

We have dealt with differences in the chromosome number of related species of organisms, and now we have to consider the relation of the forms of chromosomes to species differentiation. The ultimate structure of the chromosome is just at present a subject of intense investigation. Broadly speaking the chromosome consists of a skin, or pellicle, enclosing a structure of a spiral nature. In its developmental stages the chromosome varies in length, thus the spiral nature can account for contraction or expansion of length without loss or addition of material. During the division of the nucleus the chromosomes first appear as threads which contract to a minimum length which is characteristic under certain methods of treatment. This stage is called *metaphase* and the chromosomes then commonly have a sausage, or rod-like, appearance and may possess one or more constrictions. The absolute lengths of the chromosomes at the metaphase stage may vary from cell to cell but the length of any one chromosome relative to the others in the same cell is a constant. Each chromosome has in fact a certain individuality and so the chromosomes of an organism can often be arranged in groups according to their number, length and form based on the haploid or basic number which is a characteristic of that individual or species. Each individual or

<sup>1</sup> Blakeslee and Belling, 1924, and Blakeslee, 1930.

species thus presents what is called a *karyotype* characteristic of that individual or species. The graphical representation of the karyotype based on the morphology of the chromosome is called an *idiogram*. Hence considering the lengths of the chromosomes the idiogram can often be written down like a formula.

The idiogram, or formula, can sometimes be made use of in the determination of genetic relationship among closely related forms, and so it is of value in systematics and in collecting evidence of the evolution of species. The method has severe limitations. Navaschin and his school in 1915 were the first to make use of the karyotype and idiogram in helping to solve problems of the systematics of plant genera. The work has been continued by various workers.<sup>1</sup>

The discipline which it is necessary to develop in order to progress onwards to a full understanding of evolution is the discipline, or training, that is being worked out at present by students of cytogenetics. In this section then we will consider the developments of genetics and cytology which will enable us to approach an understanding of modern evolutionary thought. By "cytogenetics" we mean here all phenomena connected with genetics and cytology classed together which, because they give us some insight into the inheritance of variations and mutations, or because they enable us to evaluate causal theories of evolution, are connected to the central thesis of this book, which is the development of the Idea of Organic Evolution. Thus cytogenetics is here taken to include a medley of topics such as the following :— the chromosomes as wholes, the phenomena of linkage and crossing-over, the chromosome theory of heredity, multiple factor theory, sex-linked inheritance and so on. The difficulty here is to condense the vast amount of work done on these topics into such a small compass as a section in a book without omitting anything which has an important bearing on the idea of evolution. After attempting to do this, our next task will be to consider the relation of the subject to evolutionary theory. In this section historical continuity will have to give place to continuity of explanatory material.

#### 4. CYTOGENETICS

##### (a) *Deviations from Mendelian Expectations*

For some years after 1901 Mendelian investigations proceeded smoothly enough. No serious obstacles were encountered in the

<sup>1</sup> See Rosenberg, 1918; Taylor, 1924, 1925; M. Navaschin, 1925, 1926; Delaunay, 1926, 1929; Hollingshead and Babcock, 1930; Lewitsky, 1931; McCullagh, 1934; Fothergill, 1936, 1944; and many others.



interpretation of breeding experiments. Then in 1906 Bateson and Punnett,<sup>1</sup> while working with the sweet pea, obtained an  $F_2$  result which could not be explained in terms of Mendelian segregations and recombinations. They crossed a sweet pea with purple flowers and long pollen with one with red flowers and round pollen. Taken separately each pair of allelomorphic factors gave a 3 : 1 ratio with purple colour dominant to red, and long pollen dominant to the round form. The dihybrid ratio then should have been 9 : 3 : 3 : 1, but instead it was as follows :—

4,831 purple long : 390 purple round : 393 red  
long : 1,338 red round.

If the factors for purple(P), red (p) and long(L), round(l), assorted independently there should have been 4,345 with the parental combinations instead of 6,169, and 2,607 new combinations instead of the actual 783. Thus Bateson and Punnett concluded that in some of the gametes the factors for purple and long tended to remain associated together, giving an example of what they called "gametic coupling", because the results could be explained if the four types of gametes of the  $F_1$  hybrid (i.e.,  $PL$ ,  $Pl$ ,  $pL$  and  $pl$ ) were produced in the ratio of 7 : 1 : 1 : 7 instead of 1 : 1 : 1 : 1 on a basis of independent assortment. In many of the gametes the  $PL$  and  $pl$  factors were considered as remaining coupled together.

In another experiment Bateson and Punnett found that a different ratio was obtained which could only be explained on the assumption that the gametes of the  $F_1$  contained the factors in the proportion  $1PL : 7Pl : 7pL : 1pl$ . In this case the factors were thought to be repelling each other, and so the phenomenon was called *gametic repulsion*. Later (1910-11) it was suggested by Morgan that coupling and repulsion were essentially examples of what is now called *linkage*. The phenomenon of linkage, however, is part of the chromosome theory of heredity which is dealt with below.

Soon other deviations from the normal Mendelian ratios were found which, on analysis, were seen to be dependent on variation in degrees of dominance and the interaction of factors in the organisms. In the ordinary example of a cross between red-flowered and white-flowered four o'clocks (*Mirabilis jalapa*) the  $F_1$  hybrid flower is pink in colour. Here the factors for red and white have interacted so as to produce a blend or intermediate condition. Dominance here is imperfect, and the  $F_2$  ratio is 1 : 2 : 1 which, on analysis, is shown to be a modified 3 : 1 ratio.

<sup>1</sup> See Bateson, 1909; Punnett, 1923.

In other crosses an  $F_2$  ratio of 15 dominants : 1 recessive has been obtained. This is a special case requiring elaboration. G. H. Shull<sup>1</sup> crossed a variety of shepherd's purse with triangular pods with one with small ovoid pods. The  $F_1$  plants all possessed triangular pods ; in the  $F_2$  generation he obtained a ratio of 15 plants with triangular pods to 1 plant with ovoid pods. Of these  $F_2$  plants those with ovoid pods bred true, but of the 15 plants with triangular pods some bred true, some gave a 3 : 1 ratio, and others gave a 15 : 1 ratio again. This result is explicable if we assume that there are two *duplicate* dominant but independent factors which either alone or together produce the triangular form of pod.

If we represent these factors by the letters  $C$  and  $D$  and their recessive allelomorphs by  $c$  and  $d$ , then the first or  $F_1$  hybrid can be written as  $CcDd$ . In  $F_2$  the following three groups of genotypic recombinations will result :—

- (a)  $CD CD$ ,  $Cd Cd$ ,  $CD cd$ ,  $Cd CD$ ,  $Cd Cd$ ,  $cD cD$ ,  $Cd Cd$ ,  $cd cd$ , all these will breed true in the third or  $F_3$  generation.
- (b)  $Cd cd$ ,  $cD cd$ ,  $cd Cd$ ,  $cd cD$ , these will give a three to one ratio in the  $F_3$  generation.
- (c)  $CD cd$ ,  $Cd cD$ ,  $cD CD$ ,  $cd CD$ , these will give a 15 : 1 ratio in the  $F_3$  generation.

By means of this factorial representation it is seen that wherever either  $C$  or  $D$  occur singly or together the dominant effect is given in the plant. Thus the 15 : 1 ratio becomes resolved into a modified 9 : 3 : 3 : 1 (i.e., 9 + 3 + 3 : 1) ratio. Where such duplicate dominant factors are concerned the double recessive (i.e.,  $cdcd$ ) will be obtained only once in every 16 plants in the  $F_2$  generation.

Later, in 1910, Nilsson-Ehle, working with wheat, discovered triplicate factors which had a cumulative effect in the phenotypic expression of the character concerned. From his work Nilsson-Ehle developed a *multiple factor theory* which has been of great use in explaining the inheritance of size and other quantitative characters, which at first were thought to be unexplicable on a Mendelian basis. Dominance then may vary from a state of completeness to a state of true intermediacy between the parental characters. In multiple factors we are concerned with the interaction of several genes all affecting the expression of one character. For example,

<sup>1</sup> 1914, pp. 97-149.

some 50 genes affecting the distribution of chlorophyll in maize have been described.<sup>1</sup> The method by which such genes act together to produce the character is not known in detail. In the simplest cases the factors are said to be complementary if they react in the simple quantitative way of increasing or decreasing the effect of the primary gene. Other such factors may be epistatic to others if they inhibit the action of other genes. Bateson was probably the first to work out an example of epistasis when he analysed the results of breeding experiments on mice carried out by Miss F. M. Durham.<sup>2</sup> According to Bateson the black coat colour of some mice is due to a factor *B*, while the normal grey colour is due to another factor *G* "superimposed", or epistatic to *B*. Other different kinds of multiple genes are known as suppressors, modifiers, etc. Thus according to the number of genes acting, and the way in which they interact, the  $F_2$  ratio can become modified in various ways. Such deviations from the normal 9 : 3 : 3 : 1 ratio as 9 : 7, 9 : 3 : 4, 12 : 3 : 1, 13 : 3 : 1 and 9 : 6 : 1 can all be explained in terms of Mendelian factors. Multiple factors are examples of duplicate factors situated in different chromosomes, or in different parts of homologous chromosomes.

The theory of multiple factors should not be confused with the idea of multiple allelomorphs, by which is meant that a factor has several forms. A common example is the multiple allelomorphic series for eye colour in *Drosophila*. The normal eye colour is red, but a whole series of different forms exist as follows:—coral, blood, cherry, eosin, apricot, ivory, tinge, buff, ecru and white. Red is dominant to all other colours, and in any one cross one colour acts as the allelomorph of the other colour concerned.

Finally we must mention the phenomenon of *pleiotropy*. Thus far we have spoken of factors as though a single one affected a single character. This is not always so, for several cases are known in which a single gene affects several characters. A factor, indeed, may have a primary effect and several secondary effects. Mendel himself noted that plants with purple flowers also had reddish spots in the leaf axils, and seeds with grey or brown seed coats. Only a single gene is actually responsible for these character effects. Environmental conditions also affect the phenotypic action of a gene.

<sup>1</sup> Eyster, 1934.

<sup>2</sup> Bateson, 1909, p. 41.

(b) *The Chromosomes as Bearers of the Genes or Factors*

The chromosome theory of heredity was elaborated principally by the work of Morgan and his school working on *Drosophila melanogaster* which, because it possessed only four pairs of distinct chromosomes, proved to be ideal for cytogenetical investigations. The chromosome theory is a genetical theory based on cytology, or one could say interpreted according to the mechanical behaviour of the chromosomes. The basal assumption, for which the evidence is really overwhelming, is that the factors which produce the phenotypic characters as we know them are actually entities of some kind which are situated on the chromosomes in a certain linear order. Such an assumption has far-reaching implications because it means that any deviations from the "normal" type of chromosome behaviour will influence the breeding behaviour which in its turn may have an effect on variation in organisms, and so affect the *course* of evolution in such a way that the *causes* of evolutionary change may be truly detected.

As we have already pointed out, the tendency among geneticists after the rediscovery of Mendel's paper in 1901 seems to have been to regard each whole chromosome as a Mendelian factor. But this view is untenable. For it is obvious that, if the chromosomes are the material basis of heredity, then because in any organism there are very many more characters (and hence factors) than there are chromosomes, these latter must each carry several factors. In 1905 Bateson and Punnett<sup>1</sup> put forward the presence-absence hypothesis which postulated that the chromosomes each bear several factors, and further that a dominant allelomorph is due to the presence of a factor on a chromosome while the recessive is due to the simple absence of that factor on the corresponding homologous chromosome. The chromosome theory of Morgan, however, assumes that both dominant and recessive characters are represented by separate genes on the homologous chromosomes. Morgan<sup>2</sup> quoted the multiple allelomorph idea in support of his contention. The presence-absence hypothesis was then modified in the sense that the recessive was said to represent a dominant factor minus something which altered its expression. In this way multiple allelomorphs could be accounted for by a progressive quantitative diminution of the dominant factor. The most modern view seems

<sup>1</sup> 1905, p. 165.

<sup>2</sup> See Morgan, 1919.

to be that the Mendelian factors are definite entities which can exist in a number of distinct forms, or allelomorphs.<sup>1</sup> Quantitative changes in allelomorphs could then be accounted for. This view finds support in the fact that recessive factors have been known to mutate or change back to the dominant form.

Bateson and Punnett's introduction of the ideas of gametic coupling and repulsion was the first modification of Mendel's law of independent assortment to be brought forward. The phenomena which these terms described are now included in what is called *linkage*. Babcock and Clausen<sup>2</sup> define linkage as "*a relation between factors such that they are distributed to gametes in pairs of parental combinations more often than in recombinations.*" The development of the theory of linkage is chiefly due to Morgan and his school working on *Drosophila*. In this insect it has been found that the numerous factors (there are already several hundreds known) present fall into four linkage groups. These four groups correspond to the four chromosomes present in each gamete, and further it has been demonstrated that the *size* of the linkage group (i.e., the number of factors in it) bears a direct relation to the size of the chromosome to which it is assigned. For example, one linkage group is very small, containing only a very few factors, and this corresponds to the 4th chromosome of *Drosophila*, which is only a fragment compared with the others. Again, the factors of one of the groups show sex-linked inheritance. The inheritance of the sex-linked characters follows the inheritance of the sex chromosomes. This association of factors with the chromosomes in a definite way was strikingly verified by Muller<sup>3</sup>, who found a factor in some X-rayed *Drosophilae* which he was unable to assign to any of the known linkage groups. When the flies were examined cytologically it was found that they possessed a small fragment of a chromosome not present in the ordinary untreated flies. The fragment in fact added a fifth linkage group to *Drosophila*. This implies that the number of linkage groups cannot be greater than the number of pairs of homologous chromosomes, and, so far as is known, no exception has yet been found to this. Linkage groups have been worked out in some other organisms, for example, in maize and the pea.

Linkage means that if factors *AB* are present on one chromosome

<sup>1</sup> This statement is made with reservations for, with Goldschmidt's work on physiological genetics, the concept of the gene itself is changing.

<sup>2</sup> 1927, p. 126.

<sup>3</sup> 1930.

and the allelomorphs which may be  $AB$  or  $ab$  on the homologue, then when segregation occurs  $AB$  will be present in one gamete and  $ab$  in the other out of every two gametes produced. If this occurred regularly linkage would be "complete", i.e., 50% of the gametes would carry  $AB$  and 50%  $ab$ . Numerous experiments have demonstrated, however, that linkage is often "incomplete" due to the occurrence in the gametes of what are called *cross-overs*, or new combinations of factors. Using the letters used above to represent the factors, then the cross-over gametes would be written as  $Ab$  and  $aB$ . Four different gametes result, namely,  $AB$ ,  $Ab$ ,  $aB$  and  $ab$ , and thus when fertilization takes place four different phenotypes occur in the progeny. An example is seen when a normal fruit fly (*Drosophila*) with grey body and long wings is mated with one with a black body and vestigial wings. Here the  $F_1$  generation consists only of flies with grey bodies and long wings. When an  $F_1$  hybrid *male* fly is backcrossed to the female double recessive with black body and vestigial wings two kinds of flies result, namely grey vestigial winged and black long winged in equal numbers. The combination of the characters are here the same as in the parents. Linkage is then complete between the respective characters. But when an  $F_1$  hybrid *female* fly is backcrossed to a male double recessive with black body and vestigial wings the following are produced:—

Parental linked combinations		new combinations	
grey long	black vestigial	grey vestigial	black long
41.5%	41.5%	8.5%	8.5%
83%		17%	

The new combinations of grey vestigial and black long represent the cross-overs which occurred in 17% of the progeny. The process by which these new combinations arise is called *crossing-over*. Here it is assumed that when the chromosomes conjugate in meiosis an actual crossing over takes place in the pair of homologous chromosomes concerned and that a break occurs at the point of cross-over in some cases; subsequently a joining up of alternate parts of the chromosome pair takes place. Figure 2 illustrates this process in diagrammatic form.

The incidence of crossing-over enables us to give a numerical value to the amount of linkage which occurs. This value is called the linkage value. Experiments show that for each pair of factors the linkage value is constant under given environmental conditions. It was found that under certain conditions if three genes *A*, *B*, and *C* are linked together then the linkage value of *AC* is the sum of the

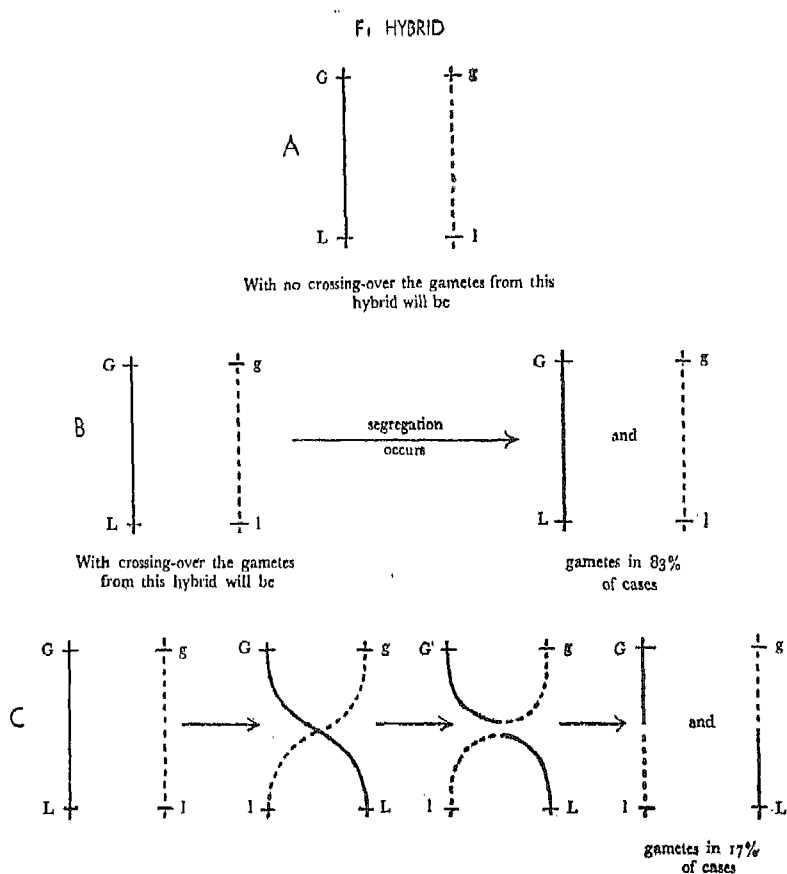


Figure 2. Legend

Diagram showing the effect on the progeny of incomplete crossing-over in the F<sub>1</sub> hybrid female *Drosophila* (obtained by crossing a normal fly with long wings and grey body with one with vestigial wings and a black body) when back-crossed with a male double recessive. For simplicity chromatids are omitted. For explanation see text.

values of  $AB$  and  $BC$ . This is the *additive theorem of linkage*.<sup>1</sup> Linkage values of different genes in the same linkage group vary from near zero to almost 50%. An actual 50% value indicates independent assortment. Given this additive theorem of linkage, and the fact that linkage values are constant for each pair of genes but vary from different genes, then one may conclude that the factors are placed on the chromosomes so as to bear a fixed distributional relationship to each other. In other words, the genes are arranged linearly on the chromosome each at a fixed locus. It is this conclusion of the chromosome theory of heredity on which modern cytogenetics is built up.

The additive theorem of linkage is only true when the genes concerned are relatively close to each other. If they are too far apart complications, such as double crossing-over, enter into the matter. The additive theorem can be stated in another way by saying that, provided the genes are not too far apart, the distance between them is proportional to the amount of crossing-over between them. Knowing the linkage values it is possible to construct maps showing the genes arranged in linear fashion on a chromosome which can be represented by a line. Such chromosome maps have been constructed showing the distribution of the large number of factors which are carried by the chromosomes of *Drosophila*. Similar ones have also been prepared for maize and the pea. The significance of this chromosome theory of heredity is that it opens up the approaches to an understanding of the nature of the gene itself.<sup>2</sup>

### (c) *Cytological Evidence for the Chromosome Theory of Heredity.*<sup>3</sup>

In the early days of Mendelism, as we have already seen, van Beneden, Henking, Boveri, Montgomery and others laid the foundations of the chromosome theory by drawing attention to the behaviour of the chromosomes in cell division and at meiosis. The matter was clinched by Sutton in 1903. Hertwig, Fol and

<sup>1</sup> See Waddington, 1939, p. 49.

<sup>2</sup> Some actual experiments on *Drosophila* illustrating a method of obtaining linkage values and determining the sequence and distance apart of selected genes on the chromosome are described in the Appendix.

<sup>3</sup> For detailed accounts of this theory see Wilson (1928, Chapter 17), Darlington (1937, 2nd Ed., Chapters 7 and 8), and Sansome and Philp (1932, Chapter 2).



Driesch in 1892 found that fertilization of sea-urchin eggs mostly resulted in a multipolar spindle at the first cleavage division.<sup>1</sup> The result of this was that a variety of monstrous larvæ were produced. Later, in 1904, Boveri, in a remarkable series of experiments of sea-urchin eggs, showed beyond doubt that it was the disturbance of the chromosomes during a multipolar division that upset the normal development of the fertilized egg which led to the production of freak larvæ. Boveri concluded that "normal development is dependent on the normal combination of chromosomes, and this can only mean that the individual chromosomes must possess different qualities." Thus Boveri showed that the chromosomes are qualitatively different in their effects on the development of characters in an organism.

The next line of support for the chromosome theory of heredity came from studies of the sex chromosome mechanism. Of this mechanism Wilson<sup>2</sup> says: "In no other field of enquiry is the close connection between cytological and genetical phenomena so readily demonstrated; nature here offers us, indeed, a series of experiments, systematically carried out on a grand scale, that afford crucial evidence concerning the causal relation between chromosomes and heredity." We can do no more than outline some of the chief points of this sex mechanism.

In 1891, von Henking noticed that half of the sperm cells of an Hemipterous insect called *Pyrrhocoris apterus* contained an extra chromatin-like body. In 1901-2, McClung<sup>3</sup> recognised this as an accessory chromosome and suggested that it was a sex chromosome, or one specially concerned in sex differentiation. Mendel was the first to suggest that sex might be concerned with segregation. The genetical ratio obtained when a dominant hybrid is backcrossed to the recessive is 1 dominant: 1 recessive and this segregation corresponds to the approximate ratio of the two sexes at birth, which is also 1 : 1. In 1907, Correns<sup>4</sup> noticed this correspondence of ratios during his experiments with hybrids of *Bryonia*. He found that in dioecious species the male produces two kinds of pollen while the female eggs were all of one kind. One kind of pollen gave rise to male plants, the other kind to female plants.

<sup>1</sup> That is, instead of a normal spindle with two poles being produced, one or more spindles with several poles were formed during the nuclear division immediately after fertilization.

<sup>2</sup> 1928, p. 742.

<sup>3</sup> 1901 on accessory chromosomes and 1902 on sex chromosomes.

<sup>4</sup> 1907, and see Bateson, 1909, for an account of Correns' work.

There was then some mechanism which made the male heterozygous, while the female was homozygous as regards sex.<sup>1</sup> The normal production of the sexes in *Bryonia* did show an exact correspondence to a backcross to a recessive. This can best be seen in diagrams where we can represent the heterozygote by  $XY$ , and the homozygote by  $XX$  :

male heterozygote	×	female homozygote
$XY$		$XX$
gametes (dissimilar) will be		gametes will all be
$X$ and $Y$		$X$
recombination will give		
1 $XX$ : 1 $XY$ .		

This suggests that there are sex factors in operation which segregate in the normal way. Correns did not connect up his results with any actual chromosomes. This seems to have been done later by Stevens<sup>2</sup> and Wilson<sup>3</sup> who found that the "genetic phenomena are exactly paralleled by certain particular chromosomes; so that the symbols  $X$  and  $Y$  may be applied to them in sex production in precisely the same manner as to the genetic factors that determine sex." These particular chromosomes are called sex chromosomes and there are now many examples of their occurrence in both animals and plants,<sup>4</sup> but they are not all of the  $XX$  and  $XY$  type.

On the chromosome theory, if indeed the sex chromosomes are truly connected with sex, certain recessive genes present on them will show a distinct type of inheritance, i.e., sex-linkage, if the  $Y$  chromosome which is different in shape is also different qualitatively from the  $X$  chromosome. Doncaster<sup>5</sup> was the first to discover what is called *criss-cross inheritance*. This type of inheritance could be correlated with the fact that he also found that the female produced eggs of two kinds, one type with 27 chromosomes,

<sup>1</sup> In 1910 Wilson substituted the terms homogametic and heterogametic for homozygous and heterozygous when applied to the sex mechanism.

<sup>2</sup> 1905.

<sup>3</sup> 1928, p. 745.

<sup>4</sup> For general references see Darlington, 1937, Chap. 9; Schrader, 1928. Wilson, 1928, Chap. 10; and Sharp, 1934, Chap. 23.

<sup>5</sup> 1908.

the other with 28, while the male gamete possessed 28 chromosomes. Here then the female is the heterogametic sex.

Such criss-cross inheritance as this, however, was first completely explained by Morgan for the fly *Drosophila*. In cultures of this fly a mutant with white eyes arose and this bred true as a recessive to the normal red-eyed colour. When a red-eyed female was crossed with a white-eyed male Morgan found that the results differed from those of the reciprocal cross. Inheritance in the  $F_2$  also differed. He was able to explain this behaviour only on the assumption that the allelomorphic factors for eye colour were carried on the  $X$  chromosomes, and that the  $Y$  chromosomes took no part in the phenotypic expression of the character. In such criss-cross inheritance a male transmits his sex-linked characters through his daughters (in which they are not shown, being recessive) to his grandsons, and the female may transmit the character to her sons and grandchildren. The sex-linked character thus alternates from one sex to the other in inheritance. In *Drosophila* the female contains the  $XX$  chromosomes, and the male the  $XY$ . We can show such inheritance diagrammatically as below if we represent the chromosomes by  $X$  and  $Y$ , and the factor for red eyes as  $R$  and that for white eyes as  $r$ , remembering that the  $Y$  chromosome plays no part in producing the character, but does affect the sex, i.e., each  $Y$ -bearing zygote will be male (see accompanying diagrams of the  $F_1$ ,  $F_2$  and the corresponding reciprocal crosses).

*The  $F_1$*

P <sub>1</sub> red-eyed female	×	white-eyed male
XX		XY
RR		r-
gametes		
X		X      Y
R		r      -
zygotes		XY
F <sub>1</sub> Rr		R-
red-eyed hybrid female		red-eyed hybrid male

*The F<sub>2</sub>*

F <sub>1</sub> red-eyed hybrid female		×	F <sub>1</sub> red-eyed hybrid male	
XX			XY	
Rr			R-	
gametes				
X	X		X	Y
R	r		R	-
zygotes				
XX	XY		XX	XY
RR	R-		Rr	r-
red-eyed	red-eyed		red-eyed	white-eyed
female	male		female	male

Notice here that the sex ratio is 1 : 1, and that the ratio of red : white is 3 : 1.

**The reciprocal cross***The F<sub>1</sub>*

P <sub>2</sub> white-eyed female		×	red-eyed male	
	XX			XY
	rr			R-
gametes	X		X	
	r		R	
zygotes				
F <sub>1</sub>	XX		XY	
	Rr		r-	
	red-eyed female		white-eyed male	

*The F<sub>2</sub>*

F <sub>1</sub> red-eyed hybrid female		×	F <sub>1</sub> white-eyed hybrid male	
XX			XY	
Rr			r-	
gametes				
X	X		X	Y
R	r		r	-
zygotes				
F <sub>2</sub> XX	XY		XX	XY
Rr	R-		rr	r-
red-eyed female	red-eyed male		white-eyed female	white-eyed male

Notice that the colour ratio is 1 red : 1 white regardless of sex, i.e., the same as a backcross ratio on to the recessive, the *XY* corresponds to the hybrid.

Since the time Morgan worked out this beautiful example very many other cases of such sex-linked inheritance have been described. The assumption in such cases is that the *X* chromosome plays no part in passing on the factors concerned. That is, it behaves as if it were inert, and there is some evidence to show that it is in fact practically so. Nevertheless, it does bear a few odd factors in some cases. Inheritance in these cases would then give a cytological confirmation of sex-linked phenomena based on the chromosome theory providing the factor on the *X* chromosome was recessive. In such a case only a *X*-bearing organism would show the character concerned. Excluding sexuality, a few cases of factors resident on the *X* chromosome have thus far been described, and, as expected, the character caused by the factor is shown only by one sex on long pedigrees. Examples are seen in the inheritance of "porcupine skin" disease and a variety of webbed toe which afflict male human beings only.<sup>1</sup>

Genetical factors are considered to go in and out of crosses unimpaired, and as the factors are borne on the chromosomes, the latter should retain their identity in and out of crosses also. A good example showing that this is so was given by M. Navaschin,<sup>2</sup> who

<sup>1</sup> See Fraser Roberts, 1940.

<sup>2</sup> 1927.

crossed *Crepis tectorum* with 8 somatic chromosomes with *Crepis alpina* with 6 somatic chromosomes. The hybrid had 7 somatic chromosomes as expected, and all the chromosomes of the parents in it could be identified by their form.

The behaviour of the sex chromosomes furnishes a good parallel of genetic and cytological segregation and recombination. Those chromosomes other than the sex chromosomes are called the autosomes. Normally the autosomic members of each homologous pair are identical in form, but in some few cases one or a few members of the complement are heteromorphic, and thus their behaviour in meiosis can be traced. They behave just like the unlike members of an  $XY$  combination, and, like the pairs of Mendelian allelomorphic factors. For instance, Miss Carothers,<sup>1</sup> working on certain beetles (*Trimerotropis* and *Circotettix*), found an unequal pair of homologous autosomes, and later several pairs of such chromosomes which segregated equally like the random segregation of factors. Further, she noticed that the longer of the two members travelled to the same pole as the  $X$  chromosome in about 50% of separations, and to the opposite pole in the other 50% of separations, which indicates independent assortment of chromosomes as well as of factors. Other workers have obtained similar results for other organisms.<sup>2</sup> Again, in hybrids of the insect *Pygera*, Federley<sup>3</sup> showed that there was no segregation of characters when the chromosomes failed to pair in meiosis. Pairing also fails in parthenogenetic organisms which show no segregation.<sup>4</sup>

The next step in the cytological demonstration of the chromosome theory is to examine the statements that the chromosomes which pair at meiosis are indeed homologous, and that the factors are situated on them. The behaviour of the  $X$  and  $Y$  chromosomes during the reduction division shows us that one chromosome from one parent actually does pair up with a corresponding chromosome from the other parent. Whatever the gene or factor really is no one knows, but it does behave as an entity in segregation. Does the chromosome give any indication of the presence of the factor?

Whatever the gene is it is of molecular dimensions, and so we cannot hope to see them on the chromosomes like beads on a necklace. During one stage of meiosis, the so-called zygotene stage,

<sup>1</sup> 1913, 1917, 1921, 1926, with review.

<sup>2</sup> Wenrich, 1917; Svetschnikova, 1928; Navaschin, 1931;

<sup>3</sup> 1913 and 1931.

<sup>4</sup> See Darlington, 1937, p. 451.

when the chromosomes are associated in pairs, they appear as long threads. Usually, these pairs of threads are so entangled and scattered within the nucleus as to make identification of each one difficult. In some few cases, however, these pairs of chromosomes can be examined individually. The individual chromosome has then been shown to have a structure made up of small dots placed linearly and connected by a fine thread. The small dots of matter are called *chromomeres*. The members of each pair are also seen to correspond with each other, chromomere for chromomere, small ones associated with small ones, large ones with large ones. Evidently here the chromosomes which are pairing are identical.

Further evidence for the pairing of identical chromosomes is only indirect, and is furnished by the behaviour of chromosomes in diploids and polyploids. Haploids are organisms with only one set of chromosomes. Hence there should be no pairing during meiosis for there are no homologous chromosomes present. Normally there is no pairing of such plants. Triploids are organisms with three sets of haploid chromosomes, tetraploids are those with four sets. Here in meiosis we expect to find associations of trivalents (three chromosomes) and quadrivalents (four chromosomes). And so we do, although pairing may be complete or incomplete.

Finally it has been suggested that the chromomeres, while not the actual factors, at least indicate their position on the chromosome. In the salivary glands of some flies, including *Drosophila melanogaster*, the chromosomes are peculiar in that they are 100 to 150 times the length of the corresponding chromosomes in other somatic mitoses; they seem to be in a permanent prophase condition. These chromosomes associate in pairs in the glands. Each one bears numerous bands placed along the chromosome (which seem to be cylinder-like). The bands occur chiefly in groups with unequal distances between them. Actually they are composed of minute chromomere-like bodies, each equally spaced within the band. When pairing occurs it is seen that exactly similar parts of the two associating chromosomes come together. By refined techniques Bridges<sup>1</sup> and Painter<sup>2</sup> have been able to map the genes on these chromosomes in *Drosophila* very accurately, while Muller<sup>3</sup> and his associates have been able to show that the smallest particle of the chromosome corresponds with the smallest chromomere as

<sup>1</sup> 1935, 1938.

<sup>2</sup> 1934, 1935, 1939.

<sup>3</sup> Ellenhorn, Prokofjeva and Muller, 1935.

shown in ultra-violet light photographs, and both of these are smaller than the unit of crossing-over, i.e., the gene.

We can end our account of the cytological evidence for the chromosome theory by considering shortly the cytological evidence for crossing-over. The evidence for this is cumulative, and obtained from nearly all aspects of nuclear study in all combinations of chromosomal arrangements. Thus a complete review is out of the question and only a short account is given. For a full treatment of the subject the reader is referred especially to Darlington<sup>1</sup> and Sansome and Philp.<sup>2</sup>

In 1909 Janssens put forward his *Chiasmotype Theory* in which it was considered that when the chromosomes paired at meiosis they broke and rejoined to different segments forming a *chiasma*. The chiasmata are the parts of the paired chromosomes which are seen to be actually joined. To Janssens then the chiasmata represented the points at which actual exchanges of chromosome parts had taken place previously. Later, in 1911, Morgan seized on this theory as the basis of his genetical theory of crossing-over on which the idea of the linear arrangement of the genes on the chromosomes is based.

Conclusive direct proof that the chiasma is in fact the point at which the chromosome pairs interchange parts has been difficult to obtain. But there is a mass of indirect evidence of great weight in this direction. Consideration of the cytology of chiasma formation, however, is much beyond the scope of this book.<sup>3</sup>

In 1931 Creighton and McClintock<sup>4</sup> working on *Zea mays*, and Stern<sup>5</sup> working on *Drosophila melanogaster* brought forward combined genetical and cytological evidence to show that genetical crossing-over is due to a cytological exchange of parts of paired chromosomes. It will be sufficient for our purpose to consider only the first of these. A plant of maize was produced with fruits showing coloured and starchy endosperm. The approximate positions of the genes for these characters on the chromosomes were known previously. The plant in question possessed a pair of heteromorphic chromosomes. One member of this heteromorphic pair was normal and carried the gene *c* for colourless endosperm

<sup>1</sup> 1937, Chapters 7 and 8.

<sup>2</sup> 1932, Chapter 2.

<sup>3</sup> A full account of the chiasmotype theory will be found in Darlington, 1937, Chapter 7.

<sup>4</sup> 1931.

<sup>5</sup> 1931.



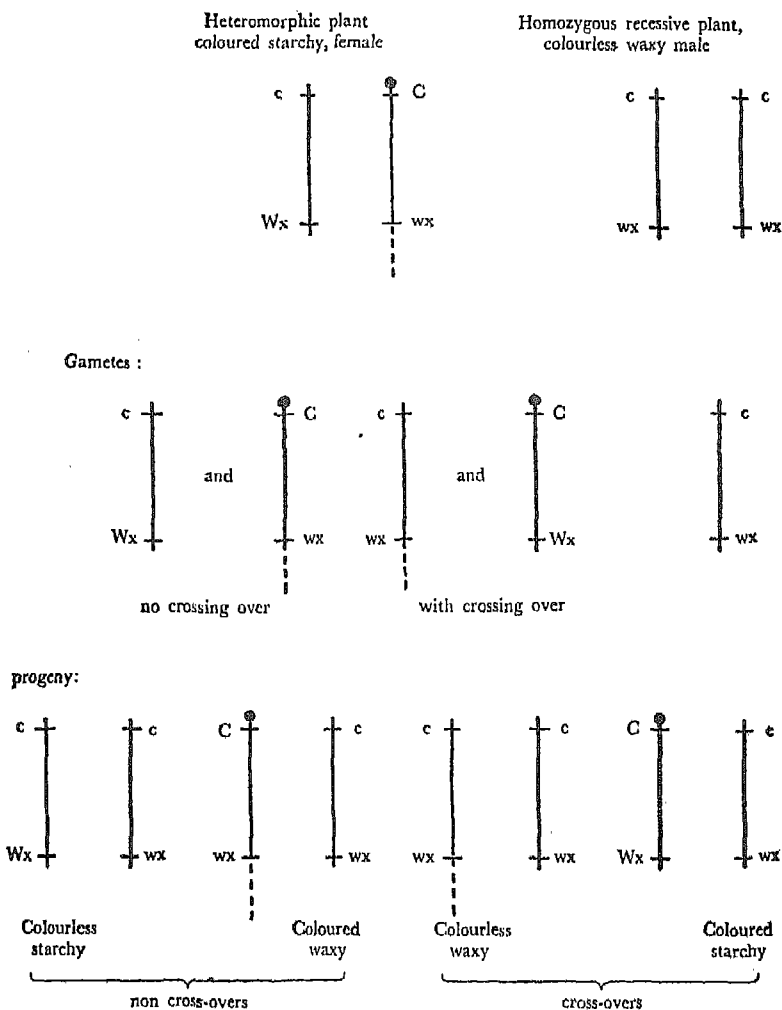


Figure 3. Legend

*Cytological demonstration of genetical crossing-over*

See full explanation in text. In the diagram, normal chromosomes are represented by black lines, the heteromorphic chromosome is shown with a black knob at one end and a translocated portion of another chromosome at the other end shown by a small interrupted line. The effects of non-crossing-over and crossing-over in the plant with this heteromorphic pair of chromosomes are clearly seen in the progeny when it is crossed with a plant without a heteromorphic pair of chromosomes. Chromatids omitted.

and the gene *Wx* for starchy endosperm. The other member possessed a large knob at one end, and, near it, the gene *C* for coloured endosperm, and also a translocated portion of a non-homologous chromosome, with the gene *wx* for waxy endosperm near it, at the other end. This plant was then crossed with a recessive homozygote with colourless and waxy endosperm, and possessing a pair of normal chromosomes carrying *c* and *wx*, and corresponding to the heteromorphic pair of chromosomes in the first plant. There were four types of progeny from this cross. Two of them resulted from ordinary segregation and recombination of the chromosomes and possessed colourless starchy and coloured waxy endosperm respectively as expected. The other two types, however, were unexpected forms with the parental characters of colourless waxy and coloured starchy respectively which, theoretically, could only arise by means of crossing-over among some of the heteromorphic pairs of chromosomes in the original coloured starchy parent. Cytologically this was demonstrated, for a clear exchange of chromosome segments had actually occurred in that the knobbed end of the chromosome carrying the gene *C* had been transferred to a normal chromosome carrying the gene *Wx*, while the other end of the knobbed chromosome bearing the gene *wx* and the non-homologous segment had been transferred to a normal chromosome carrying the gene *c*. This process is represented diagrammatically in figure 3.<sup>1</sup>

<sup>1</sup> Adapted from Sharp, 1934, p. 303.

## CHAPTER 8

### THE MODERN PERIOD CONTINUED :

#### (B) CYTOGENETICS AND EVOLUTION<sup>1</sup>

##### I. INTRODUCTION

**I**n the preceding chapter, as far as it was possible to do so, we traced the historical development from 1901 onwards of ideas regarding the mechanism of heredity. If we accept evolution as a process which has actually occurred and is still taking place at the present time, then the *experimental* study of the evolution (or history) of species becomes the study of the production of varieties of already existing species. Hence it is through heredity that we begin to attack the problems of the cause, or causes, of species change. But the study of heredity has now become the study of the behaviour of the hypothetical genes. Evolution is essentially a process of change, hence before a theory of the gene could be applied to such a process gene changes must first of all be found. Small mutations are said to represent such genic changes. Thus it is logical enough for modern theorists in biology to concentrate on the relations between small mutations and the process of evolution. In the long run, however, small changes in genes could only account for small evolutionary changes. The Modern Period has in fact been largely concerned with this development of what Goldschmidt calls "microevolution".

Experimental genetics, or the study of particulate inheritance of the Mendelian type, is actually one of the most elaborate and successful of modern studies. It justifies itself, for it is of great value to the practical plant and animal breeder in that, by use of theories which have developed from these studies, he can predict what will happen in certain circumstances. When genetics is allied to cytology, genetic theory receives confirmation at many points, and, further, and what is more important from our point of view, its scope for theoretical exploration is considerably enlarged. It is these theoretical explorations which in fact form the subject

<sup>1</sup> The word "cytogenetics" is used here in an extended sense to include any relevant matter of cytology and genetics.

matter of modern experimental work in microevolution. The subject of macroevolution has scarcely been recognised, let alone investigated, by modern cytogeneticists. They are, in fact, precluded from approaching this aspect of organic evolution, which, due to the uncertainty over the meaning of the word "species", is by far the more important side of evolution. It is in accounting for the production of the great groups of animals and plants that the whole theory of organic evolution comes up against its greatest difficulties. It is also in accounting for the origin of these same groups by any process of normal inheritance (as demanded by the theory of evolution) that cytogenetics also comes up against its greatest difficulties.

Nevertheless cytogenetics does deal with the origin of varieties and what are called species, i.e., it deals with evolution within strictly confined limits. The gene, as already indicated, is at the basis of all this modern evolutionary speculation, but this particle, whatever it is or is not, is not envisaged as acting alone. In other words, a gene does not *of itself* produce a character in an organism. The gene must then perform its work so as to bring an integration in varieties of organisms of all these essential features of the evolutionary process. In other words, the genes *must* act in conjunction with each other, and with their internal and external environments and developmental mechanisms.

Thus there arises the conception of the *genetic system* through which modern work on evolution becomes the application of cytogenetics to problems of evolutionary causation. The gene, the mathematical symbol of inheritance, has had to give way to a mechanico-physiological concept. There is, in fact, a modern school of thought which is beginning to wonder whether or not the concept of the gene is still valid. This school indeed is coming to regard the whole chromosome as the unit or particle at work in evolutionary matters.<sup>1</sup> This may mean that in the future the emphasis in genetics as applied to evolutionary problems will shift from a consideration of the mere mechanism whereby conditions are transmitted to the true physiological topic of development. Artificial "species" have been produced, we understand something about microevolution and Loeb's prophecy<sup>2</sup> has been partially

<sup>1</sup> See Goldschmidt, 1938.

<sup>2</sup> J. Loeb, 1908, p. 17, where he says: "It seems to me that the work of Mendel and de Vries and their successors marks the beginning of a real theory of heredity and evolution. If it is at all possible to produce new species artificially, I think that the discoveries of Mendel and de Vries must be the starting point."

fulfilled. But the major problems of evolution still remain unsolved.

Roughly speaking, during the first two decades of the present century, various cytological investigations were initiated which led on to further researches and results which were applied to evolutionary problems in the second and third decades. A chronological treatment of the history of evolutionary ideas during the present century would then be a patchwork of bits and pieces seemingly unconnected. So, as in the last chapter, we will seek to solve this difficulty of presentation of the subject by treating of the material in a logical, rather than chronological, fashion irrespective of the date at which it became available. The point to bear in mind is that during this century advances of evolutionary ideas went hand in hand with, and were dependent on, advances in cytogenetics.

## 2. VARIATION

Since organic evolution became a recognised principle it has been accepted that variations were the raw material of the process of change. As regards species, one can speak of a "type" and consider the deviations from the norm. This is for convenience of descriptive and experimental purposes only, for in actual fact the individuals of practically all species of plants and animals differ from their own kind in some way or another. Nowadays it is recognised that there are two main types of variation. *Modifications*, or environmental fluctuations, are produced by the action of some factor, or factors, in the surroundings of the organism. Such modifications are not inherited, and if we exclude the possibility of the inheritance of acquired characters, they are of no account in evolution. *Autogenous variations*, or simply *variations*, are produced by factors operating within the organism. This type of variation is inherited, and hence such changes in species are considered to be of evolutionary importance.

With any given variation we commonly define its type by breeding from it and observing the results. Thus of two kinds of animals of a single species with white fur, one kind may breed true, while the other may produce animals with a more normal coat colour. If it is known beforehand that the white coat colour in this species is recessive, then we can say that the former animal showed an

autogenous variation, while in the latter it was only a modification. The chief factors of the environment which produce modifications are food, light, temperature and domestication.<sup>1</sup> The chief factors giving rise to heritable variations are usually connected to the sexually reproductive mechanisms of the organism concerned. In some cases, however, a change which produces an heritable variation takes place in a somatic growing tissue of a plant; they are called *bud variations*.

Variations are, of course, the starting point of most breeding experiments, and the aim of cytogenetics is to give a rational explanation of the principles underlying the production of variations, that is, to relate the observed inherited change in a character of some mechanism operating in the germ plasm. The application of the results obtained to the question of the origin of species constitutes the contribution of cytogenetics to problems of evolutionary causation.

In the preceding chapter we dealt with some cases of variations produced by observable changes in reproductive cells, or by the movements of genes in those cells. In this connection distinctions are often drawn between inter-varietal and inter-specific variations. There is a good deal of evidence to show that there is little real difference in their nature.<sup>2</sup> The distinction, however, matters little so long as there is no clearcut delimitation of species and varieties. It is convenient at this point to give an arbitrary classification of the primary sources of variation. The remainder of this chapter will then be directed to the part they are said to play in the evolution of species.

The changes occurring in the germ plasm which give rise to autogenous variations may be grouped as follows:—

- (a) changes involving whole sets of chromosomes,
- (b) individual chromosome aberrations,
- (c) internal chromosomal re-arrangements, involving the phenomena of reduplication, deletion, translocation and inversion,
- (d) new combinations of genes,
- (e) gene mutation.

The basic assumption made here is that a gene, or group of

<sup>1</sup> See Sinnott and Dunn, 1925, for examples.

<sup>2</sup> See Haldane, 1932d, Chapter 3.

genes, act together in the organism to produce in some way the characters of that organism. The important point, however, is not so much, does a certain re-arrangement of the germ plasm produce a simple variation, but does it affect the *course* of evolution? We can say that the course of evolution of *species only* should be affected if a new type of organism arises which is able to maintain itself unchanged. It is unnecessary to deal further with changes due to new gene combinations, for these are continually occurring in every act of sexual reproduction. As regards the effect of new gene combinations on evolution, sexual reproduction becomes important only when due to it some new form different from the parents is produced. Hence, as long as the idea of the gene is at the basis of the science of genetics, genes themselves represent the building blocks of evolutionary changes, and, as a corollary, new combinations of genes which are adaptive represent the pattern cut into the blocks, giving a distinctive appearance to the whole structure.

### 3. CHROMOSOMAL CHANGES

#### (a) *Changes involving whole sets of chromosomes*<sup>1</sup>

In this section we have to consider the effects of polyploidy and hybridity on the variation and evolution of species. The occurrence of polyploid series of chromosome numbers has already been described (Chapter 7). The first case of polyploidy was described by Lutz<sup>2</sup> in 1907, and concerned *Oenothera gigas* with 28 chromosomes, which arose as a mutation from *Oenothera Lamarckiana* with 14 chromosomes. Since then so many polyploid series have been found among plants as to suggest that the phenomenon is of very common occurrence. Statistical investigations have shown some interesting features in connection with polyploidy. For instance, O. Winge in 1917 found that among the chromosome numbers of flowering plants there was a very high frequency of multiples of basic numbers, and a low frequency of prime numbers. In 1931 A. Fernandes<sup>3</sup> drew up frequency graphs of 2,413 species of flower-

<sup>1</sup> Full accounts of polyploidy, amphidiploidy and related topics are given by Goodspeed and Bradley (1942), Darlington (1937), Sansome and Philp (1932), and Waddington (1939).

<sup>2</sup> Lutz, 1907, and later Gates, 1908.

<sup>3</sup> 1931, from Darlington, 1937, pp. 229-232.

ing plants with chromosome numbers between 3 and 100. From these it was evident that not one peak occurred at a prime number (i.e., at 7, 11, 13, 17, etc.), while the largest numbers of classes of species were found among the basic factors (i.e., among 8, 12, 16, 24). Winge suggested that new species arise by polyploidy, and Fernandes' work suggests that those running in multiple series are selected. R. A. Brink<sup>1</sup> pointed out in 1935 that the facts of polyploidy have been of great evolutionary significance among plants. And, indeed, the study of this phenomenon has shown us that it must have played a great part in the production of varieties. Indeed, in experimental work on polyploidy some new "species" have been produced.

Polyploids can be classified in various ways, but for our purposes we may make use of the following distinctions. The chromosome sets of any plant may be similar or dissimilar. In the first case the plant is said to be an autopolyploid, and in the second case an allopolyploid. This distinction is important, for in meiosis in autopolyploids the chromosomes can pair up in groups of two or four or more, while in allopolyploids, because the sets of chromosomes are not homologous, little or no pairing should occur (the actual degree of homology may vary and also the amount of pairing). As a result the gametes in allopolyploids will tend to be non-viable, and the plants sterile. It is with this latter group that we are chiefly concerned.

As a result of his studies on polyploidy, Winge<sup>2</sup> was able to put forward his theory of "indirect chromosome binding" which gave an explanation of the production of new species through the agencies of polyploidy and hybridization. The idea of the theory is very simple. If a species A, with a chromosome set  $A_1, A_2, A_3, A_4$ , etc., is crossed with a species B with a dissimilar set of chromosomes, viz.  $B_1, B_2, B_3, B_4$ , etc., Winge supposed that, on the basis of experience, in the hybrid AB these chromosomes would not pair up, meiosis would be irregular, and the hybrid would be sterile. He suggested that the need for pairing among chromosomes in meiosis would stimulate the chromosomes to double in the hybrid. Each chromosome would then have a homologue, so that complete pairing would occur, with the result that the hybrid would breed true. This can be represented diagrammatically as in Figure 4.

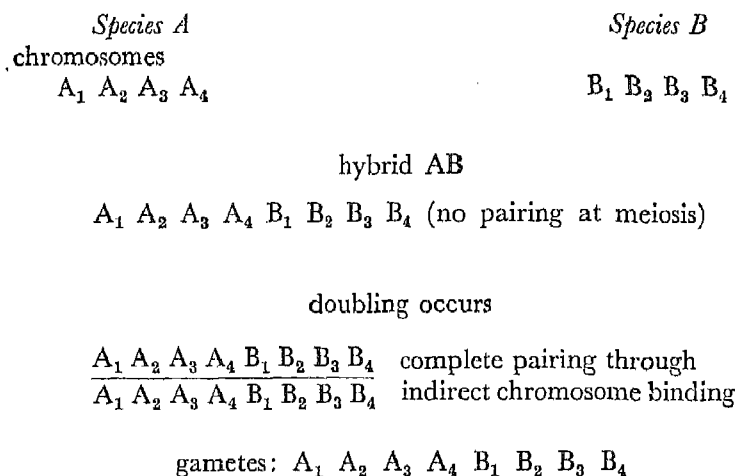
<sup>1</sup> 1935, p. 100.

<sup>2</sup> 1917.



Figure 4

Diagram illustrating indirect chromosome binding



Plants produced from such a hybrid would then be allopolyploid because they would contain full sets of dissimilar chromosomes ( $A_1 B_2$ , etc.). Such plants in which this doubling has occurred are usually called *amphidiploids*, and their condition is referred to as *amphidiploidy*. According to Darlington<sup>1</sup> the first known case of this occurred in the moth *Pygaera*, but usually the first completely worked out example quoted is that of the new "species" *Nicotiana digluta* produced by Clausen and Goodspeed<sup>2</sup> in 1925 from a cross between *N. tabacum* and *N. glutinosa*. Doubling occurred in the  $F_1$  hybrid giving rise to *N. digluta*. This was a hexaploid with perfectly regular reduction divisions. Soon afterwards a series of amphidiploids arose spontaneously in experimental hybrid cultures. In 1926 Tschermak and Bleier produced the fertile amphidiploid *Aegilotriticum* from *Triticum durum* and *Aegilops ovata*. Karpechenko in 1927 produced *Raphanobrassica*, the amphidiploid from a cross between a radish and a cabbage. Both of these are fertile hybrids obtained by crossing species in different genera. In 1928 Buxton and Newton obtained *Digitalis Mertonensis* from *D. ambigua* and *D. purpurea*. There is now quite a long list of such

<sup>1</sup> 1937, p. 183.

<sup>2</sup> 1925.

amphidiploids. T. H. Goodspeed and Miss Bradley<sup>1</sup> in a review of the subject give a list of 124 such plants reported as arising through doubling in a hybrid. The reverse process to allopolyploidy was carried out by Wettstein<sup>2</sup> who broke up a species of the moss genus *Physcomitrium* into its two presumed parental sets of chromosomes.

The examples mentioned so far all arose in cultures. It remains to be seen whether allopolyploids occur in nature. Müntzing<sup>3</sup> claims to have been the first to synthesize a plant which resembled a distinct natural species. He crossed *Galeopsis pubescens* with *G. speciosa*. Among the plants of the subsequent F<sub>2</sub> generation was a triploid and this was backcrossed to the *pubescens* parent. Among the progeny of this cross was an allotetraploid which was called *Synthetic Galeopsis Tetrahit* because it was indistinguishable from the naturally-occurring *G. Tetrahit* in its morphological, genetical and cytological characteristics. The conclusion to be drawn from Müntzing's work is that the origin of the natural plant of *Galeopsis Tetrahit* was similar to that of the synthetic one.

Müntzing's cross was a distinct demonstration that, in nature, allopolyploidy may give rise to distinct systematic species. Before this, however, several cases of natural species arising by chromosome doubling had been described. A few examples are given below.

In 1924 Blackburn and Harrison showed that the wild rose, *Rosa Wilsonii*, was an allohexaploid derived from *R. pimpinellifolia* and *R. tomentosa*. In 1881 Focke considered that *Aesculus carnea* was a true-breeding natural hybrid from *A. hippocastanum* and *A. pavia*, while in 1929 A. Skovsted gave a very convincing cytological demonstration that this plant had probably arisen from these supposed parental species by hybridization and doubling. *Primula Kewensis* is a horticultural plant which is a hybrid between *Primula floribunda* and *P. verticillata*, each with 18 chromosomes. The hybrid should possess the same number of chromosomes, but Digby in 1912 found that it had 36 somatic chromosomes. Newton and Pellew<sup>4</sup> later found that it had arisen through doubling which occurred in a branch of the first hybrid.

Sansome and Philp<sup>5</sup> consider that allopolyploids are of very common occurrence in nature, i.e., that they have played a great part in the evolution of plant species. On *a priori* grounds this

<sup>1</sup> 1942.

<sup>2</sup> 1932.

<sup>3</sup> 1930 and 1932.

<sup>4</sup> 1929.

<sup>5</sup> 1932.

is probably correct, but the statement is difficult to prove directly. The reason for this is that natural allopolyploids do not remain static, but evolve within their group. Their cytological behaviour, however, sometimes provides evidence of their remote origin by amphidiploidy. This evidence is provided by what Darlington<sup>1</sup> calls the differential affinity of the chromosomes. For example, in the straight hybrid *Primula Kewensis* the 9 chromosomes from *P. floribunda* pair with the 9 from *verticillata*. When doubling occurs in the hybrid to produce an allotetraploid, pairing is then between identical chromosomes, *floribunda* chromosomes pair with *floribunda*, and *verticillata* with *verticillata*, to give 18 regular pairs, or bivalents. Sometimes, however, an irregularity is noticed in that one, two or more quadrivalents are formed in which 2 *floribunda* chromosomes are associated with each other and with 2 paired *verticillata* chromosomes in each group of four. This differential affinity is taken to indicate a previous affinity between *floribunda* and *verticillata* which is to be expected, otherwise hybridization would have been unsuccessful in the first place.

There is cytological and genetical evidence to show that in the course of time structural and other internal chromosomal changes may occur in the original parents of amphidiploids. *Primula Kewensis* is a recent introduction, and the original parents show complete pairing of chromosomes but only partial pairing in the amphidiploid doubled product (there would be complete pairing in this if 9 quadrivalents were formed).<sup>2</sup> The presence of irregularity in the form of a few quadrivalents leads to sterility and in point of fact the progeny of recent allopolyploids show all grades of fertility range. On the other hand in allopolyploids of old standing differential affinity of chromosomes should be at a minimum, for, as species age, it is possible that their chromosomes change structurally and lose their pairing qualities. In old species like *Triticum vulgare* and *Avena sativa* an occasional quadrivalent is found which is said to be due to the pairing of chromosomes derived from the ultimate ancestors. Cytological investigations of these matters have led Darlington<sup>3</sup> to say: "It is therefore

<sup>1</sup> 1937, p. 198.

<sup>2</sup> There are only a few examples of complete pairing in amphidiploids, but one may be given. Although the straight diploid hybrid produced by crossing *Crepis rubra* with *C. fetida* shows almost normal pairing in meiosis, Poole (1931) found that the amphidiploid which arose from it sometimes shows the presence of a full set of five quadrivalents.

<sup>3</sup> 1937, p. 226.

probable that the occurrence of structural changes in the two separated sets (i.e., of the original diploid parental chromosome sets) in the normal course of variation is a more important source of differentiation between the chromosome sets, and thus of the evolution of allopolyploids in general."

In the analysis of polyploid species cytological evidence of the kind given above is very persuasive, but not decisive. It requires to be supplemented by as wide a variety of crosses and backcrosses as possible, so as gradually to eliminate the possible interpretations until only one remains, in much the same way as a doctor diagnoses his cases. Besides, many of the cytological arguments are tainted with teleology. Confirmatory evidence of the evolution of some plant species by means of allopolyploidy is needed, and has been provided in an interesting way. The mere production of a new type of plant has little significance for evolution unless the new arrival can maintain itself in nature, or perhaps eliminate its parent types during the struggle for existence. Two cases in which this has occurred are now known.

*Spartina Townshendi* (The Rice Grass) appeared suddenly towards the end of the nineteenth century. In appearance it is intermediate between *S. stricta* (with 56 chromosomes) and *S. alterniflora* (with 70 chromosomes). Huskins<sup>1</sup> examined the plant cytologically and found that it possesses 126 chromosomes, and probably arose by doubling in a hybrid between *S. stricta* and *S. alterniflora*. At first *S. Townshendi* was a rare but vigorous plant. At the present time, however, it is very prevalent along certain parts of the coasts of England; and where it comes into contact with its *stricta* parent it soon eliminates it; while the other parent is restricted in its locality. In the other case J. Clausen<sup>2</sup> has shown that *Penstemon neotericus* probably arose as an amphidiploid from *P. lactus* and *P. azureus*. The plant is very successful in nature in contact with its supposed ultimate parents.

Recently, amphidiploids have been produced artificially by application of certain chemicals, or by other special treatments, to hybrid plants. For example L. F. Randolph<sup>3</sup> produced a few tetraploid maize plants by application of temperatures near to the maximum temperature for survival. Bartolucci<sup>4</sup> obtained one or

<sup>1</sup> 1931.

<sup>2</sup> 1933.

<sup>3</sup> 1932.

<sup>4</sup> 1939.

two amphidiploids by centrifuging germinating seeds of a hybrid between *Nicotiana tabacum* and *N. sylvestris*. Among the chemical inducers of chromosome doubling colchicine must be reckoned as the most important at present. This chemical, obtained from the roots of a species of *Colchicum* (meadow saffron), was first used on plants by Dustin, Havas and Lits, and since then a large number of amphidiploids have been produced by its use.<sup>1</sup> The following chemicals have also been tried on plants with a certain degree of success—chloroform, acenaphthene, chloral hydrate, naphthalene, phenanthrene, and some arsenic and lithium compounds. So far no correlation has been obtained between the presence of colchicine or other compounds in the soil and the incidence of supposed natural allopolyploidy.

As regards these artificial amphidiploids the question arises whether or not they are new species. Generally speaking they combine the characters of both their parents, but they usually show some new morphological characters and also physiological and chemical changes which may have a more far-reaching effect.<sup>2</sup> The fact remains that amphidiploids are true-breeding hybrids differing from their parents, and if these were distinct species, there would seem to be little genetical or systematical reason why amphidiploids should not be labelled as new species. Indeed, in the case of the intergenetic hybrids between the cabbage and radish, or between wheat and rye, we must regard them as synthesized species, otherwise our whole system of classification would become meaningless. E. Anderson<sup>3</sup> considers that there is no valid reason why even a new genus, family or order, should not arise through amphidiploidy. Perhaps this is an example of over-optimism for it must be emphasized that such polyploids as these, although they are new, are still but re-arrangements of the chromosomes and genes already present in the original parents. In them nothing intrinsically new, in the sense of new genes, has been produced.

Stebbins<sup>4</sup> reviews the subject of polyploidy in the evolution of plants. He finds that the distribution of polyploids throughout the plant kingdom is very irregular, and, except in a few families, it does not show any correlation with any phylogenetic schemes. He reviews the situation in the genus *Crepis* in some detail and

<sup>1</sup> See Dermen, 1940, and Goodspeed and Bradley, 1942.

<sup>2</sup> See L. F. Randolph, 1941, p. 355 *et seq.*

<sup>3</sup> 1937.

<sup>4</sup> 1940, p. 59.

concludes that although the polyploid complex<sup>1</sup> has existed since tertiary times, the polyploid members have not produced any new characteristics. The polyploid complex thus tends to be a closed system. New polyploids which arise in the group "are new variations on old themes"; they do not represent new lines of evolution. Stebbins<sup>2</sup> concludes that "the evidence from the plant kingdom as a whole, therefore, suggests that polyploidy has been most important in developing large, complex and wide-spread genera; but that in respect to the major lines of evolution, it has been more important in preserving relics of old genera and families than in producing new ones."

Bearing in mind the fact that there is little to show the method of the evolution of the major groups, this is surely a dangerous admission for an evolutionist to make. It is tantamount to saying, "here we have a method which admittedly produces many new species, but these species do not count in evolution".

Mere addition of chromosome groups may not produce new arrangements of chromosomes and their constituent genes. This will be brought about by mutations or sudden changes in genes. Morgan,<sup>3</sup> the originator of the gene theory, in fact considers that gene mutations are alone of any value in the processes of organic evolution. Most mutations are recessive to the normal. In an amphidiploid each set of allelomorphs is represented four times, i.e., by AAAA or BBBB. If one of these mutates to *a*, a recessive gene, it will be overshadowed by the three dominant allelomorphs in each case, i.e., by AAA or BBB. Before the recessive character could become expressed the plant would have to be homozygous for the mutated gene, i.e., it would have to be of the constitution *aaaa* or *bbbb*. Quite obviously, such a tetraploid homozygous form would be produced much less frequently than in the case of the corresponding diploid plant. In fact, Haldane<sup>4</sup> has demonstrated mathematically that the chances of obtaining a homozygous recessive of this type decreases rapidly in the order diploid—tetraploid—hexaploid—octoploid. Stadler<sup>5</sup> had previously shown that the mutation rate in wheat produced by means of X-rays decreases in the same order. C. L. Huskins<sup>6</sup> points out,

<sup>1</sup> That is, a combination of auto- and allo-polyploidy throughout the species of the genus producing an intricate network of relationships.

<sup>2</sup> 1940, p. 65

<sup>3</sup> 1916, 1926, 1932.

<sup>4</sup> 1930.

<sup>5</sup> 1930c.

<sup>6</sup> 1941.

however, that the mutations so far noted in polyploids have not been proved to be due to single gene mutations. They are mostly due to chromosome aberrations affecting large parts of, or even whole, chromosomes and in polyploids the unbalance so produced among the chromosome sets will not necessarily affect the viability of the plant concerned. Such aberrations, or changes in chromosome balance, are not considered to produce any really new characteristics. Huskins contends that only qualitative or gene changes can do this, and these have not as yet been demonstrated in polyploid plants.

We can conclude this section by remarking that although polyploids are of common occurrence in nature, and although hybrids between them are often able to breed true, there is little agreement about the part played by them in evolution. Generally speaking, those strict geneticists who hold the view that gene mutations are of primary importance in the production of new species assign polyploidy to an unimportant and minor role. It is admitted that gene mutations and polyploidy can both operate in the production of new species. Evidently there are at least two kinds of species, one of which is important in evolutionary differentiation and the other unimportant.

### (b) *Individual Chromosomal Aberrations*

The occurrence of aneuploid, or polysomic, plants has already been mentioned in chapter 7. These chromosome "mutations" usually arise through irregular distribution of chromosomes during meiosis, which causes the resultant gametes to have varying numbers of chromosomes. In the simplest cases some of the gametes will possess an extra chromosome ( $n+1$ ). Hence, when fertilization takes place the zygote and the plant which develops from it will possess  $2n+1$  chromosomes. Polysomic organisms are found in both plants and animals.

In *Datura stramonium* the haploid number of chromosomes is 12, and the complete series of twelve  $2n+1$  forms have been found. Each of these simple trisomics, as they are called, is sufficiently different from the parent plant, and from their sister trisomics, to warrant the use of a separate name for each. Eleven out of the twelve possible trisomics have been found in the tomato,<sup>1</sup> and they have also been produced in maize and in *Crepis*.

<sup>1</sup> Lesley, 1928.

At meiosis in such plants the presence of the extra chromosome leads to irregularities in chromosome separation, with a corresponding alteration of gametic and zygotic ratios. Hence inheritance in trisomic plants, and even more so in higher polysomics with several odd chromosomes, does not follow ordinary Mendelian rules, for they do not breed true and cannot become fixed in nature. Thus they are not considered to be of great evolutionary importance.

#### 4. INTERNAL CHROMOSOMAL ARRANGEMENTS

It is known from genetics and cytology that certain structural changes can occur in the internal arrangement of individual chromosomes so as to interfere with the normal linear order of the genes. These changes may be classified as below :—

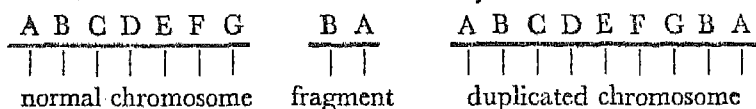
(a) *Deficiency*. Here a small portion of a chromosome, or a block of genes, becomes lost from a chromosome, or a part of the chromosome becomes inert.

A normal chromosome with the genes *ABCDEFGG* may thus become *ABCDE* due to loss of *FG*.

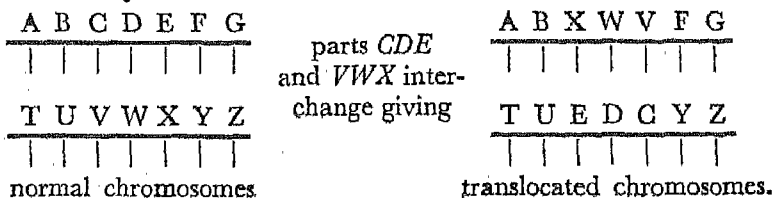


(b) *Duplication*. Here an extra portion carrying genes already present on the chromosome may be added to it.

A normal chromosome *ABCDEFGG* may become *ABCDEFGGBA*.

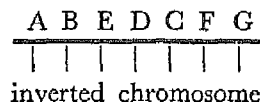
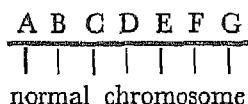


(c) *Translocation (reciprocal)*. This is often called *segmental interchange*. Here two chromosomes interchange parts. Chromosomes *ABCDEFGG* and *TUVWXYZ* may become *ABXWVFG* and *TUEDCYZ*.





(d) *Inversion*. Here a portion of a chromosome becomes completely inverted reversing the order of genes within the block. A chromosome *ABCDEFGG* may become *ABEDCFG*.



It is not necessary for our purpose to go into the details of the ways in which these structural changes in chromosomes occur.<sup>1</sup> The important point is that such inter-genic changes, as Darlington calls them, bring different genes into different spatial relationships with each other. It is necessary, however, to point out that there is a fundamental difference between the various types. Inversions and translocation merely alter the arrangement of the genes so that the phenotypic expression of characters may or may not be altered. On the other hand, in deficiencies genes are lost, whereas in duplications genes are added to the chromosome complement, with the result that the phenotype is usually altered. Deficiencies and duplications then are immediate sources of variation, while translocation and inversions are only potentially so. The part played in evolution by this latter type of change is aptly put by Darlington,<sup>2</sup> who says: "Inversions or other structural change, can float in a species, picking up, as it were, by chance combinations with different genes the elements from which a cleavage of a higher order will ultimately develop in the species: a cleavage, that is, depending on the isolation of zygotes and not of parts of their chromosomes." A similar belief was expressed at the same time by Muller,<sup>3</sup> who, however, also points out that those who imagined that internal chromosomal arrangements led immediately to the production of new species had an over-simplified view of the matter. He describes a number of factors which militate against the spread of intergenic changes in a species.

Structural changes in chromosomes have been induced in organisms by exposure to X-rays, by means of chemicals, centrifuging, and the like. It is most probable that similar types of chromosome change also occur in nature, but these are only

<sup>1</sup> A masterly and detailed account of chromosomal changes is given by Dobzhansky (1941, Chapter 4), to which book the reader is referred.

<sup>2</sup> In *The New Systematics*, ed. J. Huxley, 1940, p. 147.

<sup>3</sup> In *The New Systematics*, ed. J. Huxley, 1940, p. 213.

recognised by inference from the behaviour of the chromosomes at meiosis. The presence of ring-multivalent chromosomes, chromosome bridges between the poles, and so on, are taken to indicate that the chromosomes concerned have been altered structurally.

#### (a) *Deficiencies and Deletions*

Deficiencies may exist in homozygous or heterozygous form, and the size of the deficient portion of the chromosome may vary. It is generally accepted that they could play no part in evolution, for, as East<sup>1</sup> says: "It is hard to imagine how the loss of chromatin could have been an important means of advancing organic evolution." For instance, Demerec,<sup>2</sup> working on the X-chromosome of *Drosophila melanogaster*, found 62 lethal changes in the gene loci investigated. Genetic tests showed that 53 of these were deficiencies, and this was confirmed for 18 of them by a study of the salivary gland chromosomes. He further showed that the deficiencies involved only a small number of genes. Indeed, it seems probable that some of the ordinary lethal gene mutations described for *Drosophila* are really very small deficiencies. The lethality of deficiencies may begin to affect the organism quite early in development. For instance, D. F. Poulson<sup>3</sup> found that deficiencies of parts of X-chromosomes in *Drosophila melanogaster* affect the processes of embryonic development adversely. Again, Demerec<sup>4</sup> has shown that cells in which deficiencies occur frequently become disorganised.

However, a few of the deficiency mutations in *Drosophila* are not lethal when homozygous. It has been suggested<sup>5</sup> that in these cases the unbalance consequent upon such a loss is buffered by the presence of a duplicated segment for the same genes as the deficiency but situated elsewhere in the chromosome.

#### (b) *Duplications*

There are two kinds of duplications: a fragment of a chromosome may be translocated to another chromosome, or a block of genes may be present twice in the same chromosome. These latter types

<sup>1</sup> 1936, p. 147.

<sup>2</sup> 1935.

<sup>3</sup> 1937 and 1940.

<sup>4</sup> 1936.

<sup>5</sup> Muller, 1935.

are called *repeats*. The recent salivary gland technique has enabled Bridges<sup>1</sup> to show that groups of similar genes occurred at two different portions of the one chromosome, and this has been observed in a number of species of *Drosophila*. Some mutations have arisen which are causally referable to duplication. In 1925, A. H. Sturtevant showed that a mutation called Double-Bar, which arises from the mutant type Bar of *Drosophila melanogaster*, is due to duplication. Furthermore, Bridges<sup>2</sup> also showed that the mutant gene Bar is itself due to a duplication of several genes. The loci of these genes are known, and from the effect on the phenotype Sturtevant was able to discover what is called the *position effect*. It was found that two flies with different Bar expression contained the same number of Bar genes. The phenotypic difference could only be accounted for<sup>3</sup> on the basis of the different position occupied by the Bar genes in the respective chromosomes.

Duplications are considered to be of some importance in evolution, but the evidence for this is all indirect and inferential. Few positive results have so far emerged from investigations in this new field. Duplications immediately upset the balance of genes, and create a new reaction mode which may produce a new phenotype. Obviously duplication is one method of increasing the number of genes leading to an increase in the chances of the production of divergent mutations of possible use in evolution.

### (c) *Translocations*

In experiment and in nature a number of cases have arisen which require special interpretation. In cytogenetics the basic assumption is made that only similar and specific parts of homologous chromosomes will pair at meiosis. Assuming this theory of specificity of chromosome pairing, then cytological findings may be interpreted in terms of chromosome pairing. In the ordinary straight diploid plant the homologous chromosomes pair up at meiosis; thus, if the chromosomes present are represented by AABCC . . . etc., then these will form the following pairs  $\begin{smallmatrix} A & B & C \\ A & B & C \end{smallmatrix}$  . . . etc., at meiosis. Many organisms, however, are not

<sup>1</sup> 1935.

<sup>2</sup> 1936.

<sup>3</sup> That is, assuming the truth of the gene theory.

straightforward diploids, and in meiosis various combinations of chromosomes are found. Thus, instead of bivalents, we may find chains of chromosomes forming trivalents, quadrivalents, pentavalents, etc., or rings of chromosomes of varying number. If we assume that the chromosomes forming multivalent associations are homologous either as wholes or in parts, then their association enables us to examine the relationships of various forms, and also to interpret many natural occurrences without violating the general chromosome theory of heredity. Thus the presence of odd ring formations leads us to infer that the chromosomes associated have interchanged parts or blocks of genes. The only other alternative is to suppose that in such associations non-homologous chromosomes have come together. The latter view would clearly contradict the general deductions from genetics and the chromosome theory.

Interchanges of parts of chromosomes are brought about by translocations. These have been produced and identified in *Drosophila*<sup>1</sup> and maize<sup>2</sup> and a few other organisms. That they have occurred in a fairly large number of plants and presumed species hybrids, among them *Pisum sativum*,<sup>3</sup> the pea, *Campanula persicifolia*,<sup>4</sup> *Matthiola incana*,<sup>5</sup> *Tulipa spp.*,<sup>6</sup> *Paeonia*,<sup>7</sup> *Datura*,<sup>8</sup> *Oenothera*,<sup>9</sup> and many others, has been inferred from cytological evidence. With the exception of *Drosophila*, few translocations have been found in animals. White,<sup>10</sup> however, has described a case in a wild population of grasshoppers (*Metrioptera brachyptera*).

Individual plants may be either homozygous or heterozygous, for a translocation (or several translocations), and their breeding behaviour will be affected accordingly. In the translocation homozygote, for instance, the gametes will carry the gene (or group of genes) concerned only once, while in a translocation heterozygote at least six kinds of gametes will result. Some

<sup>1</sup> Stern, 1929.

<sup>2</sup> McClintock, 1930, and Cooper and Brink, 1931.

<sup>3</sup> Hakansson, 1929, 1931, and 1934; Sansome, 1932a; and Lamprecht, 1939.

<sup>4</sup> Darlington and Gairdner, 1937.

<sup>5</sup> Philp and Huskins, 1931.

<sup>6</sup> Upcott, 1937.

<sup>7</sup> Müntzing, 1938.

<sup>8</sup> Only a selection of references are given here: Belling, 1925; Blakeslee, 1928, 1929, 1932; Bergner, Satina and Blakeslee, 1933; Blakeslee, Bergner and Avery, 1937.

<sup>9</sup> Only a selection of references are given here: Darlington, 1929, 1931; Cleland and Blakeslee, 1930; Cleland, 1931.

<sup>10</sup> 1940.

of these will be normal, some deficient in genes, and some will carry duplicate genes<sup>1</sup>.

The idea of translocation was first postulated by Blakeslee<sup>2</sup>, who used it to account for the peculiar behaviour of races of *Datura stramonium* and some other species. *Datura stramonium* possesses 12 pairs of chromosomes which can be identified by their genetical and cytological behaviour. Normally, at meiosis, they form 12 bivalents. The plant is widely distributed in the U.S.A., Europe, West Africa, Australia and South America, where it forms geographical races which are alike phenotypically, but, as their breeding behaviour shows, they have chromosome complements which differ structurally. Altogether about 40 such "Prime" types, as they are called, have been described by Blakeslee and his co-workers. Blakeslee chose a race common to the U.S.A. as an arbitrary standard, and when this is crossed with the other geographical races, or these are crossed among themselves, the hybrids resulting show a varying number of ring chromosome associations. As the chromosomes are individually distinguishable, they have been given a "formula" by numbering the ends of the chromosomes. The normal arbitrary strain thus possesses 1.2: 3.4: 5.6: . . . . 21.22: 23.24: chromosomes. Structural changes in the various races and the hybrids is then indicated by interchange of these numbers among the chromosome complements. For instance, one race shows chromosomes 1.18 and 2.17 instead of the normal 1.2 and 17.18, while another shows 11.22 and 12.21 instead of 11.12 and 21.22. Apparently these respective sets of chromosomes have interchanged segments in the prime races. Assuming that homologous parts of non-homologous chromosomes pair up at meiosis, then figure 5 readily shows how the structural hybrids between the races would possess a ring of four chromosomes at meiosis.

Likewise, the application of the idea of translocation to *Oenothera* has enabled the peculiar genetics of this plant to be satisfactorily interpreted and at the same time has given an explanation of the occurrence of large numbers of rings in meiosis. The number of rings varies, but in one type (*Oenothera augustissima*) all 14 chromosomes present form one large ring: in *Oenothera Lamarckiana* there are one bivalent and one ring of 12 chromosomes. In spite of this

<sup>1</sup> See Muller and Settles, 1927, and a general account in Dobzhansky, 1941, p. 298 *et seq.*

<sup>2</sup> 1922.

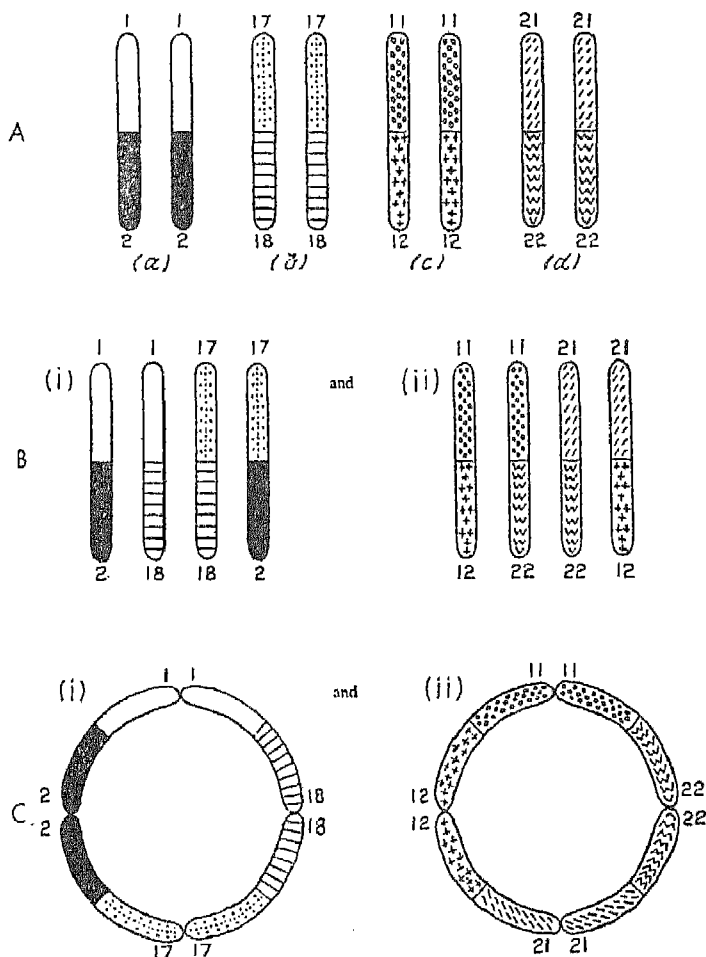


Figure 5. Legend

*Translocation in Datura*

In *A* (a), (b), (c) and (d) represent four pairs of normal homologous chromosomes; the ends of these are marked differently and numbered. In *B* (i) translocation has occurred between two of these pairs of chromosomes with ends 1-18 and 17-2. In *B* (ii) a similar translocation has occurred, producing chromosomes with ends 11-22 and 21-12. In meiosis like ends of chromosomes associate together, hence in each case (i) and (ii) the four chromosomes concerned will associate, forming a ring of four chromosomes, as shown in *C* (i) and (ii) respectively. (After Blakeslee).

high degree of irregularity the *Oenotheras* breed true, and it appears that they are permanent translocation heterozygotes the condition of which is maintained due to the fact that the homozygous translocations are lethal. Theoretically translocation heterozygotes should produce at least 50% of unbalanced gametes with duplications, deficiencies, deletions, etc., which are usually lethal. Several workers have reported 50% sterility in ring forming plants. For example Blakeslee<sup>1</sup> found 50% pollen abortion when various races of *Datura* were crossed to the standard race; while Cooper and Brink<sup>2</sup> discovered five races of *Zea mays* which showed the presence of rings and 50% abortion of pollen. Again, Sansome and Philp<sup>3</sup> found there were two races of the edible pea with ring formation and also 50% sterility. In maize, hybrids between the translocation races and the normal type were partially fertile, and a certain relation was obtained between the actual number of translocations and the degree of sterility.

Dobzhansky<sup>4</sup> points out that, since the duplication and deficiencies in 50% or more of the gametes of translocation heterozygotes are lethal, then their "reproductive potentials" are lowered. Hence in wild populations such structural hybrids will be subjected "to a negative selection pressure tending to decrease their frequencies and eventually to eliminate them altogether." Referring to the persistent nature of the prime types or geographical races of *Datura*, J. Huxley<sup>5</sup> writes: "This is in effect a form of isolation and should eventually give opportunities for mutation and selection to produce visible differences between the various chromosomal types." Here then we have two different interpretations. We can assume that these *Daturas* are quite old and should by now have become phenotypically different from the normal race if such cytological phenomena have any bearing on their evolution. On the other hand, Dobzhansky indicates that no negative selection pressure operates on translocation homozygotes, and in fact, if these form a majority in the population the parent condition will be acted on by selection.

For translocation forms to become effective in evolution an effective sterility barrier between the translocated race and the parental type must be created. If this exists then such races may

<sup>1</sup> 1929.

<sup>2</sup> 1931.

<sup>3</sup> 1932.

<sup>4</sup> 1941, p. 115.

<sup>5</sup> 1942, p. 90.

provide potential material for evolution to work on through subsequent mutations and crossings. Direct evidence for this is lacking.

(d) *Inversions*

In 1926 Sturtevant found that in certain cultures of *Drosophila melanogaster* there was a cross-over reducer for certain loci; this was explained by assuming that a certain section of the third chromosome had become inverted, i.e., had suffered rotation through 180 degrees. Chromosomes in which this process occurred were unable to form normal cross-overs with their homologues. Later, in 1931, he found that, in flies homozygous for the inversions, the frequency of crossing-over was restored, but new linkage groups had emerged. In 1933 McClintock was able to show a characteristic looping of the paired chromosomes concerned in the early meiotic division of maize. At a later stage (anaphase) when the other chromosomes had passed to the poles a chromatin bridge remained connecting up the two separated masses of chromosomes, while nearby a chromosome fragment lay unattached. This was taken as an indication that an inversion had occurred in one of the chromosomes concerned, in the looping. Since then such chromatin bridges have been reported in *Matthiola incana*,<sup>1</sup> *Tulipa*,<sup>2</sup> different races of *Campanula persicifolia*,<sup>3</sup> *Tradescantia*,<sup>4</sup> *Agropyron*,<sup>5</sup> and in many others. They have also been found in animals such as some grasshoppers,<sup>6</sup> and in squirrels.<sup>7</sup> Inversions were first found in species hybrids by Müntzing<sup>8</sup> in the cross between *Crepis divaricata* and *C. dioscorides*. They have since been found in others. Actual demonstrations of inversions have been made in the giant chromosomes of the salivary gland cells of *Diptera* (flies). These salivary gland chromosomes are of immense relative length and show a definite structure of either plate-like discs, or of small dots of matter. The position of these structures corresponds to the position of the genes on the genetical chromosome maps. When pairing takes place these chromosomes normally associate point by point. But where pairing

<sup>1</sup> Philp and Huskins, 1931.

<sup>2</sup> Upcott, 1937.

<sup>3</sup> Darlington and Gairdner, 1937.

<sup>4</sup> Darlington, 1937.

<sup>5</sup> Ostergren, 1940.

<sup>6</sup> Darlington, 1936.

<sup>7</sup> Köller, 1936.

<sup>8</sup> 1934.



fails in parts of the chromosomes a comparison of the unpaired parts often shows differences in the arrangement of the discs or dots. In this way inversions can be identified on the actual salivary gland chromosomes by an alteration of their pattern.

For some time *Drosophila miranda* and *D. pseudobscura* were a puzzle to geneticists. Outwardly and chromosomally they were identical, and could only be distinguished by statistical analysis of characters such as size. They differ also in some physiological features such as the time taken to reach maturity. They cross with each other, but the hybrids are sterile whereas the males are abnormal. When the salivary glands were examined it was found that the chromosomes either failed to pair at all, or only paired in very complex associations. Point to point comparisons of these chromosomes showed that large numbers of inversions and translocations have occurred in them. In fact Dobzhansky and Tan<sup>1</sup> state that about one hundred such chromosomal changes must have occurred to produce the salivary gland chromosomes of these two types. Types like these are best described as "genetic species". Tan<sup>2</sup> further showed that the two races A and B of *Drosophila pseudobscura*, which cannot be distinguished externally and further produce sterile hybrids, are differentiated only by several inversions as seen in the salivary gland chromosomes. Dobzhansky and Socolov<sup>3</sup> have likewise described two chromosomal races of *Drosophila azteca* distinguishable only by such inversions.

From the evidence available then it is plain that such re-arrangements of genes are of very common occurrence in species, both wild and cultivated. Indeed there is one species (*Paris quadrifolia*) where nearly all the chromosome pairs show the presence of inversions by the formation of bridges.<sup>4</sup> This alone suggests that inversions have played a great part in the production, if not of species, at least of varieties and geographical races. Inversions were first recognised by their property of suppressing crossing-over. The amount of interference with crossing-over will vary according to the size of the inverted chromosome segment, for where the inversion only involves a few genes crossing-over may occur more or less as usual. But where the inversions involve large numbers of

<sup>1</sup> 1936.

<sup>2</sup> 1935.

<sup>3</sup> 1939.

<sup>4</sup> Geitler, 1938.

genes crossing-over in these regions may be entirely suppressed. In inversion heterozygotes the result will be to reduce fertility. On the other hand, an inversion homozygote should be relatively fertile with its like, but sterile with its ancestral form, for here the inverted segment will prevent chromosome pairing. Darlington<sup>1</sup> seems to have been the first to point out that this was a form of isolation keeping the parental form and the inversion homozygote apart. Further evolutionary divergence will result if mutations occur in the inverted portions of the chromosomes.

Summing up, it is recognised that inversions and translocation do not add anything new to the germ plasm (as they are merely re-arrangements), at least according to the current gene theory, but they may, under favourable circumstances, form "genetic species". Further, when heterozygous they lead to sterility and thus tend to become extinguished, but when homozygous and genetically isolated the "genetical species" may persist. Again, morphologically such forms show little, if any, differences which are of value in species determination. Finally, they seem to be of common occurrence in nature. (It is suggested here that statistical analysis may show that the aberrants may vary around a mean much as modifications do.) Consensus of opinion among cytogeneticists seems to regard them as of great importance in evolution. Dobzhansky calls them one of the mainsprings of evolution, while J. S. Huxley<sup>2</sup> regards them as important but only as secondary agents in speciation. These views, of course, are founded on the idea that the gene or factor is an entity responsible for the characteristic form and features of an organism. Goldschmidt considers that it is the chromosome *pattern* which is of importance, and so to him the important agents in evolution are those inversions and translocations which alter the pattern of the chromosome. It will be necessary to deal with Goldschmidt's views in some detail later.

## 5. THE ULTIMATE UNIT OF THE CHROMOSOME

### (a) *The Gene: General Features*

We have not, as yet, dealt with the gene as a separate structure. In this section we wish to give a general account of the nature of genes. It is necessary to point out, however, that a consideration

<sup>1</sup> 1937.

<sup>2</sup> 1942, p. 333.

of gene mutations properly belongs here, but for convenience of arrangement we have delayed dealing with this topic.

Warmke<sup>1</sup> makes a distinction between new genes and gene mutations which are merely changes in already existing genes. It is apparent that new mutant genes could provide the first steps in diversity which is essential to evolutionary advance.

Nevertheless the number of possible gene changes operating through inheritance is large enough to provide an enormous amount of variation. For example, if we assume that every new gene change doubles the number of possible combinations theoretically available, then the 400 or so known mutations of *Drosophila* allows for  $2^{400}$ , or about  $10^{120}$ , conceivable new combinations.<sup>2</sup> Only a minute fraction of this astronomical number of possible combinations are actually known. The real point, however, is that it has not so far been shown that any new combination of old or new genes has led to the production of variations which are sufficiently large to warrant the assumption that in time an accumulation of them would produce an entirely new organism completely different from its ancestors.

Indeed we may say that the investigations of this period, which only opened in 1901, have just begun the study of experimental evolution. It is, therefore, too much to expect that the major evolutionary problems have already been solved. What has been accomplished is that the problems of heredity have been tackled in the hope that their solution would provide a causal explanation of the way in which evolution occurs. But the intense study of heredity has led to the idea of the gene with the result that many modern evolutionary speculations are based on this idea. Genes have been defined in several ways, but always in such a way as to satisfy the requirements of experimental genetics. For instance, while the idea of the gene as a unit particle was at its height, F. A. E. Crew<sup>3</sup> gave the following definition which fitted in very well with the new ideas which were beginning to be advanced at that time. He defined a gene as "a particular state of organization of the chromatin at a particular point along the length of a particular chromosome. It is a particular area or locus of the chromosome in a particular state. One particular condition of this chromatin can be replaced by others and with each change another gene

<sup>1</sup> 1941, p. 346.

<sup>2</sup> See Sewall Wright, 1931, and also Gulick, 1938.

<sup>3</sup> 1927, p. 733.

appears." For all general purposes this definition may be accepted as a working basis.

Mendel's postulated factor was a simple thing. A certain factor produced a certain character, and that was that. Then the factors were thought to be parts of the chromosomes. Later, as factual exceptions to the original Mendelian expectations multiplied, this view had to be seriously modified. Nowadays it is regarded as heresy to talk of a gene for tallness, or a gene for red eyes. Huxley<sup>1</sup> points out that what is investigated in any given genetic experiment is a *character-difference*, not a character, and this difference is expressed in terms of genes. We saw that the deviations from Mendelian expectations in experiments were interpreted as showing the presence in the germ plasma of modifying, complementary, epistatic, multiple, etc., genes. That is, that genes interact in the organism to produce external or phenotypic effects. Thus has arisen the idea of the "gene complex". It is this gene complex, or internal environment, which supplies the basic conditions necessary for the development of certain character-differences. It means that actually many genes operate to produce a character in an organism. In other words, the original Mendelian idea has been thrown over. The idea of the gene complex obviously facilitates the interpretation of particularly difficult cases of particulate inheritance.

The concept of the interaction of factors has been stabilised by the work of Timofeeff-Ressovsky,<sup>2</sup> who has shown that different gene complexes of local races of *Drosophila funebris* alter the expressivity (the degree of expression), the penetrance (the frequency of the effect) and the specificity (the qualitative variation in the nature of the effects) of several genes. Earlier, the same worker<sup>3</sup> obtained pure-breeding stocks of a mutant of *Drosophila funebris* called "*radius incompletus*," which varied in its phenotypic expression according to the genetic environment in which it occurred.

The genes and gene complexes, however, have also to contend with the external environment, which is a variable factor. It has, in fact, been found that variations in the environment may alter the form of a character of an organism (for example, submerged leaves of a semi-aquatic plant often differ profoundly in shape from the aerial leaves of the same plant). This can only mean

<sup>1</sup> 1942, p. 62.

<sup>2</sup> 1934, and see Waddington, 1939, pp. 163 and 188-191, for an account of this.

<sup>3</sup> 1927.

that either a gene (or genes) may have several phenotypic expressions according to the conditions of the environment, or several genes are responsible for the shape of leaves, some of which come into effect under one set of external conditions and some under another set. Temperature is an external factor which shows great variation, and Collins<sup>1</sup> showed that there may be a recessive gene in barley which prevents the formation of chlorophyll at low temperatures (6° C.). At higher temperatures (18° C.) the plants were quite normal: while at temperatures between these two extremes, various intermediate conditions were noticed. Morgan<sup>2</sup> found a dominant sex-linked character called "abnormal abdomen" which was only expressed when the flies were living under damp conditions. Under dry conditions even flies homozygous for the gene concerned remained normal. Again, Child<sup>3</sup> found that the development of a set of bristles in *Drosophila melanogaster* depended on the temperature during the larval life of the insect.

The idea of the gene complex has also enabled some selectionists to attempt to reconcile the idea of the essential continuity of organisms inherent in Darwinian theory with the idea of the essential discontinuity inherent in mutation theory. J. S. Huxley,<sup>4</sup> who is in the vanguard of so-called "Darwinians", for instance, contends that although actual mutations are abrupt changes nevertheless evolution is a continuous process, for each new mutant gene as soon as it appears is *buffered* by other changes in the gene complex, which modify its action until it becomes adjusted to the needs of the organism. "In any case," Huxley says, "what evolves is the gene-complex; and it can do so in a series of small, if irregular steps, so finely graded as to constitute a continuous ramp." L. P. W. Renouf,<sup>5</sup> in a critique of Huxley's book from which the above quotation was taken, bids us beware of "deductive" statements of this kind.

### (b) *The Chemical Nature and Function of Genes*

Several suggestions about the chemical nature of genes have been put forward. The idea of the gene is an abstraction, but as genes act physiologically, and so long as their behaviour in the

<sup>1</sup> 1927.

<sup>2</sup> 1915.

<sup>3</sup> 1935.

<sup>4</sup> 1942, pp. 67-78.

<sup>5</sup> 1944, p. 33.

mutation process, whatever they are actually, enables us to identify them as particles on chromosomes, then it is obvious that it is through the chemistry of the chromosome that we will be able to gain further insight into the nature of genic action and function. At the beginning of the century, Bateson had attempted to give the genetical factor a material basis by his presence-absence theory which we have already mentioned. Morgan, in his theory of the gene, does not consider that the presence-absence idea is a necessary, or even warranted, deduction from the facts of genetics. In Morgan's theory the absence of a gene is considered to be impossible; the occurrence of reversible recessive mutations supports this contention, for how could something which is absent revert to a former condition? A portion of a chromosome might, however, become inert, either temporarily or permanently, but the normal Mendelian ratios would then be upset. Hagedoorn<sup>1</sup> was probably the first to suggest that genes are autocatalysts, i.e., catalysts which reproduce themselves at the end of a chemical reaction. Several other hypotheses have been suggested. For example, Eyster<sup>2</sup> brought forward a genomeric theory which postulated that every gene is composed of several sub-genes each of which produces a slightly different quantitative effect on the organism. A similar idea, called *step allelomorphism*, has also been advocated by several workers, chiefly of the Russian school,<sup>3</sup> who suggest that the sub-genes are arranged in a definite linear order or pattern on the chromosome, corresponding to a pattern of effects in the organism.

From a *priori* considerations genes are said to possess the following characteristics as enumerated by Goldschmidt:—<sup>4</sup>

- “1. It is a highly active substance and is potent in very small quantities.
2. The substance of the gene is doubled before each cell division; it is therefore capable of assimilation and growth.
3. The gene is able to undergo a definite, sudden, and in many cases reversible change, called mutation.
4. The mutated gene is perpetuated in the same way, is as stable as the original gene, up to the moment of formation of another mutation.”

<sup>1</sup> 1911.

<sup>2</sup> 1924 and 1928.

<sup>3</sup> Serebrovsky, 1927 and 1929; Levit, 1930; Dubinin, 1929; Agol, 1931.

<sup>4</sup> 1938, p. 282.

Goldschmidt further points out that Hagedoorn's assumption that the gene is an autocatalyst can account for the first two points; but in order to explain the last two points, special assumptions are necessary. The simplest assumption to make is to regard the gene as a single molecule or group of molecules. If we accept this assumption then mutations can be imagined as arising in the following ways, as enumerated by Goldschmidt:—<sup>1</sup>

1. By a change in quantity of the gene.
2. By one molecule changing into another.
3. By a side-chain in the molecule being replaced by another.
4. By formation of a stereoisomer.
5. By polymerization or formation of chain molecules.

Actually only a beginning of the study of chromosome chemistry has been made, but recently several suggestive results have been obtained. Genetics teaches us that the chromosome is differentiated along its length. Hence, if genes have a chemical basis, the chemical composition of the chromosome must change linearly. In the chromosome, two types of substances have been shown to be present. These are (a) a desoxyribose nucleic acid, and (b) one or more proteins. Although in only a few cases has an actual chemical analysis of nuclei been made, it seems likely that the composition of the nucleic acid is too constant to account for the linear differentiation of the chromosome. Hence the proteins remain as the possible sources of the genes. Chemical analyses of the nuclei of fish sperm had shown the presence of proteins called protamines and histones, and it became generally considered that substances of these types formed the basic structure of chromosomes. But, from the genetical point of view, these proteins are too simple in their chemical composition to account for the behaviour of genes. In 1943, Stedman discovered a more complex protein, which he called *chromosomin*, and his work indicated that other complex proteins may be present within nuclei. It is possible, then, that the linear genic differentiation along the length of the chromosome may be due to different arrangements of the amino-acid groups of these more complex proteins. There is some evidence to show that the proteinaceous framework of the chromosome can expand and contract like a fibrous protein, such as fibroin, and that the

<sup>1</sup> 1938, p. 283.

nucleic acid present serves to hold the protein framework rigid in the metaphase chromosome. On the basis of this and other evidence Goldschmidt thinks that the whole chromosome behaves as a unit in heredity like an immense protein chain which could have a definite pattern like that postulated by Bergman for fibroin. In such a view, the reactions of the amino-acids of the chain would constitute the functions of the gene. A mutation could arise by any breakage or re-arrangement of the protein chain which altered the fundamental pattern, resulting in a new phenotype. In Goldschmidt's view, then, the gene as a discrete entity ceases to exist. Finally, it is possible that there may be a special "gene substance" as yet undetected; variations in the structure of this substance could perhaps account for the linear differentiation of the chromosome.

## 6. CRITICISMS OF THE GENE THEORY AND OF THE CHROMOSOME THEORY

### (a) *Introduction and General Criticisms*

The particulate theory of heredity which we call the theory of the gene is not based on a new idea. It derives from Weismann's theory of the germ plasm by way of Spencer's "physiological units" and Darwin's "pangens". Many of the arguments advanced against Weismannism may also be applied to the gene theory. The modern theory, however, differs from these earlier ones in two chief regards. Firstly, the gene theory is susceptible to mathematical treatment, and secondly, it postulates that every living cell of the organism contains a full set of the genes, which are all derived from the fertilized egg or zygote. This postulate, however, raises a major difficulty when the theory is applied to the problems of developmental physiology, because it is difficult to see how the phenomena of embryonic segregation can be explained in terms of genes which are the same in every cell of the organism. In fact, little or no true headway has been made in genetical investigations which aim at showing how the gene actually brings about the transformation of a microscopic comparatively homogeneous egg into a complex heterogeneous organism. As Lillie<sup>1</sup> says: "We should of course be careful to avoid the implication that in its

<sup>1</sup> 1927.



future development the theory of the gene may not be able to advance into this unconquered territory (i.e., developmental physiology). But I do not see any expectation that this will be possible even in principle, so long as the theory of the integrity of the entire gene system in all cells is maintained. If this is a necessary postulate of the gene theory, the phenomena of embryonic segregation must, I think, lie beyond the range of genetics." The gene theory holds that the gene, at least in the soma, is stable, its action constant and final. On the other hand, developmental physiology has to deal with an essentially plastic organism.

As the theory of the gene became extended, due to the discovery of more and more deviations from the simple ratios first found by Mendel, and as we have already indicated, the emphasis gradually changed from the gene as producing a character to a gene as part of a reaction system responding to its environment. The gene theory became a theory of genetic systems by such discoveries as multiple allelomorphs, factor interaction, etc. In theory, this amounts to a process of reduction of the *number* of operative genes which catalyse the reactions responsible for what is called development. This extension of the gene concept does narrow the gap separating the two disciplines of genetics and developmental physiology, but the essential problems still remain. Further, if genes are regarded as some kind of autocatalytic enzymes which act by initiating chemical reactions, then we must remember that, by definition, in physiology an enzyme is highly specific in the reactions which it catalyses. To reduce the number of genes and invoke a genetic system does not fit in with the idea of the gene as a particle, and in particular a catalyst of an enzyme nature, for, surely, the number of reactions which bring about development is immense, and of exceeding great variety. There is, then, a gap between a stern gene concept and an equally stern and deterministic developmental concept, when the two should dovetail into each other. The fundamental difficulty confronting geneticists is that the concept of the gene is a truly morphological one. This morphological conception is of great value to biological science, and has given rise to many brilliant pieces of research fruitful in results, but, as Stroer<sup>1</sup> says: "However important and interesting these researches may be, they have not led us any further as regards insight into the nature of life and organisation."

The gene theory, again, seems to clash with physiology in another

<sup>1</sup> 1936, p. 58.

way. Studies of eggs long ago revealed that the constitution of the cytoplasm is important for normal development. Boveri, Loeb, Jenkinson<sup>1</sup> and others even went so far as to suggest that the main characters of large groups like orders, families, and even species, were caused by the cytoplasm, and that the nucleus only produced varietal differences. Cases are known in which cytoplasmic factors of the egg seem to influence development. For example, the first generation hybrid obtained from the cross between *Epilobium luteum* female and *E. hirsutum* male is different from that obtained from the reciprocal cross. If this difference is caused by the cytoplasm of the female *luteum* parent, then repeated crossings with the pollen of the *hirsutum* plant should rapidly reduce it until the descendants all look alike. Michaelis,<sup>2</sup> however, found that the influence of the *luteum* cytoplasm was still noticeable even after 14 generations of crosses of the *luteum* hybrid with *hirsutum* pollen.

Cytoplasmic inheritance has also been described in mosses by Wettstein,<sup>3</sup> in the insect *Lymantria* by Goldschmidt<sup>4</sup> and in several other organisms by other workers.<sup>5</sup> Goldschmidt comes to the conclusion that there are true cases of cytoplasmic influence upon the genic action in heredity and development. He finds that the influence of the cytoplasm becomes greater the less the affinity between the species concerned in the original crossing. It is not settled, however, whether this influence is purely cytoplasmic, or is itself controlled by genes which gradually affect the maternal cytoplasm until after several generations they bring it under their complete control, so that the sporadic effects of the cytoplasm are no longer noticeable. This phenomenon was called *dauermodifikation* by Jollos<sup>6</sup> who first described it in some *Protista* after treating them with heat.

The application of the principle of uniformity to the gene theory forces its strict upholders, or those who believe in the overwhelming influence of the nucleus in heredity, to consider that these cases of cytoplasmic inheritance or influence so far discovered are of no importance in evolution, and leads them to postulate the existence

<sup>1</sup> 1917, p. 18.

<sup>2</sup> 1937.

<sup>3</sup> 1926, 1927, 1928 and 1937.

<sup>4</sup> 1931, 1934a.

<sup>5</sup> Reviews of the subject are given by East (1934), Goldschmidt (1934a), Wettstein (1937), and a good account by Waddington (1939).

<sup>6</sup> 1921, and see also Haemerling, 1929.

of genes which brings about cytoplasmic action.<sup>1</sup> E. E. Just,<sup>2</sup> however, probably expresses a common opinion when he writes: "For me it is difficult to divorce nucleus (and chromosomes) from plasma. Nor can I conceive that even the most ardent supporter of the gene theory does so. The cell is a unit: the nucleus influences the plasma, and plasma the nucleus. The cell reacts as a whole. Sharply to divorce these two constituents of the protoplast is to make them abstractions."

Another criticism of the gene theory from an essentially physiological viewpoint of sex and hybridity is supplied by H. W. Jensen<sup>3</sup> who doubts the existence of sex chromosomes in flowering plants. Jensen admits that from a genetical point of view the idea of sex chromosomes is quite logical, but he remarks: "Is it not possible that the transfer of these genetical values, called factors or units, from the purely mathematical realm to a specific portion of an organic structure (such as a chromosome) may entail a larger jump than is now contemplated?" As the sex chromosome mechanism accepted by geneticists is purely mechanical, he contends that the theory must find its support in purely mechanical foundations. And this is where it fails. After examining the supposed cases of sex chromosomes in fifty angiosperms in which they have been described, he contends that these phenomena can be adequately and better explained by investigation of the initial hybrid nature of the plants concerned. The sex chromosomes are in fact a phenomenon of hybridity: "they are simply one of the by-products of organic evolution."<sup>4</sup>

### (b) *Special Criticisms*

Many biologists, and others, have at times criticised the gene theory either from a general or particular viewpoint without giving any sustained criticism of it, for indeed to accept the theory in its entirety requires a large amount of credulity in the acceptor. The ramifications of the theory in its logical developments stretch the methodological limits of Natural Science to the uttermost. After the general criticisms given above there is no need to do more than to give a selection of special or sustained criticisms which

<sup>1</sup> For example, see Morgan, Bridges and Sturtevant (1925, p. 84), Morgan, 1927, pp. 7-9, 208-209 and 654-655; 1926 b, pp. 487-515.

<sup>2</sup> 1932, p. 73.

<sup>3</sup> 1940, p. 69.

<sup>4</sup> H. W. Jensen, 1940.

attack the general idea of the gene or the chromosome theory. Thus we will consider the views of W. Johannsen, C. Dobell, and E. S. Russell. Other important critics are Yves Delage (1903) H. Stieve (1923), J. Dembowski (1926) and E. Rabaud (1937).

(i) *The Criticisms of W. Johannsen*

W. Johannsen introduced the word "gene" into genetics to designate the factors postulated by Mendel and his successors. In a clear, but short, paper<sup>1</sup> he discusses the limitations of the gene concept. He points out that the word has a morphological connotation, and when applied to the organism in a physiological or chemico-physical sense it becomes superfluous, for what are dealt with are "*reactions of the constitution*" of the organism which implies that there are no unit-characters at all. Johannsen points out too that what we deal with in genetics are differences; a 3:1 ratio represents one point of difference, a 9:3:3:1 ratio represents two points of difference and so on.<sup>2</sup> Hence the important problem to solve is to ascertain whether the genes really represent local deviations from the "normal" state in the chromosome. Johannsen asks: "Is the whole of Mendelism perhaps nothing but an establishment of very many chromosomal irregularities, disturbances or diseases of enormously practical and theoretical importance but without deeper value for an understanding of the "normal" constitution of natural biotypes? The Problem of Species Evolution does not seem to be approached seriously through Mendelism, nor through the related modern experiences in mutations."<sup>3</sup>

Here at once Johannsen lays his finger on the crux of the matter by indicating that the mere genetic study of minor differences between species, many of them abnormal, have little, if any, significance in evolution, or the real process responsible for the transformation of one species into another. This admission seems to imply that the true species, or natural entity called by this name, is a clear cut category of individuals in which minor differences are unimportant.

<sup>1</sup> 1923.

<sup>2</sup> R. Ruggles Gates, 1933, claims to have been the first to point out that "a gene represents a difference—a fact so obvious that it is in danger of being overlooked."

<sup>3</sup> 1923, p. 140.

The comparative unimportance of these minor differences which do Mendelize leads Johannsen to consider that the important characters of organisms are inherited *in toto*. He notices that, in spite of numberless mutations and crossing experiments, Morgan's Pomace flies still remain Pomace flies whether or not they have lost all of their "good" genes. In other words the essential features which make a *Drosophila* fly an insect of this species are continuously inherited without change. In Johannsen's opinion this indicates that there is a central "something" operating in heredity, and he thinks that this, whatever it is, is probably not divisible into separate units.

### (ii) *The Criticisms of C. Dobell*

Dobell<sup>1</sup> offers a detailed criticism of the chromosome theory of heredity on the basis of chromosome behaviour in the *Sporozoa*, a group of parasitic unicellular organisms. He first of all points out that this theory is dependent on three older ones the truth of which it takes for granted. These are the theories of (1) nuclear dominance, (2) the individuality of the chromosomes and (3) the continuity of the chromosomes. Thus he<sup>2</sup> says: "If any one of these basic assumptions could be effectively negated, the doctrine that the chromosomes carry or contain factors or developmental determinants would have to be regarded, it seems to me, as either false or undemonstrated—no matter how we define 'factors' or 'determinants' and no matter how we conceive them to be specially associated with chromosomes." To him the theory rests upon a positive correlation between a particular character and a particular chromosome in an organism.

Dobell's researches dealt with species of *Aggregata*. *Aggregata eberthi* is a sporozoan parasite which possesses 6 haploid chromosomes. In the life history of this one animal there are four different types of individuals—males, females, sporonts and schizonts, excluding gametes, young forms and reproductive stages. In his argument Dobell selects a particular character (sex) and a particular chromosome, *a*, which he assumes contains the factors determining that character. Actually the chromosomes are individually distinguishable and the *a* one is the longest. In the life cycle of the parasite the spore germinates to produce a sporozoite which

<sup>1</sup> 1925.

<sup>2</sup> 1925, p. 180.

possesses one *a* chromosome. The presence of the *a* chromosome is here associated with the absence of sex. The mature schizont produces young merozoites, each with one *a* chromosome. The young merozoites develop to become males and females each still with one *a* chromosome. Here the presence of one *a* chromosome is correlated equally with maleness and femaleness. Male merozoites give rise to spermatozoa while females merozoites give rise to ova. Actually gametes have no sex and so again chromosome *a* is correlated with absence of sex.

These gametes fuse in pairs and the resultant zygote develops to become the sporont but the two *a* chromosomes separate in the first division of the zygote nucleus. The sporont is completely asexual and again the presence of the *a* chromosome is correlated with absence of sex. Here the life cycle is completed.

Dobell<sup>1</sup> remarks that from this behaviour "it is clear that the presence of the chromosome *a* is not correlated with the character sex in *A. eberthi*; for it is equally present in males and females and in organisms without sex." The same argument applies to each of the other five chromosomes and to any of the characters of the organism. Thus Dobell is led to the general conclusion that there is no correlation between the presence of any character and the possession of any particular chromosome, or particular part of a chromosome. He finds that "In *Aggregata* we see great individual diversity associated with apparently complete identity of chromosome constitution. From generation to generation the forms and functions of the animal change in an orderly sequence, while the chromosomes remain unchanged. They are the constants in a varied series of developmental stages."<sup>2</sup> According to Dobell it follows from this that there is no reason why we should postulate that the chromosomes are concerned with hereditary transmissions.

Arguments such as these can be applied to any haploid organism, and Dobell also applies them to the problems of cellular differentiation in diploid organisms taking *Drosophila* as an example and dealing with the XY sex chromosome mechanism and the character red eye, the gene for which is said to be carried by the X chromosome. His analysis of the supposed relation between character and chromosome and gene in these diploid organisms leads to the conclusion that what is shown "is merely a general correlation

<sup>1</sup> 1925, p. 183.

<sup>2</sup> 1925, p. 184.

between the presence of a certain *set* of chromosomes in *all* the cells of the body and the presence of all the characters displayed by that body *as a whole*: but this implies no more than that the chromosomes themselves are a bodily character—in the same sense that a red eye or a testis is a bodily character—and tells us nothing regarding the functions of the chromosomes and their ‘causal’ or other relations to the other characters.”<sup>1</sup>

### (iii) *The Criticisms of E. S. Russell*

In *The Interpretation of Development and Heredity*<sup>2</sup> E. S. Russell states a case for the organismal interpretation of living things in contrast to the prevalent mechanistic one. He is thus led to deal with Morgan’s particulate theory of heredity.

Like Gates and Johannsen, Russell points out that the gene theory deals with differences. As the differences found in experiment are discontinuous then Morgan assumes that they are particulate. This is a difficulty which has long been known to the geneticists, who have many times defended their position. But, in spite of statements to the contrary, Russell<sup>3</sup> says that the gene theory “in effect ‘reifies’ or endows with material existence what are merely differences and it does this by postulating a gene for every heritable difference found.” When developed logically the theory built on this postulate leads to very great complications, such as the creation of upwards of thirty allelomorphs for eye colour alone in *Drosophila*.

Such postulation of genes for character differences in fact leads to incredible results. For it becomes necessary to postulate as many normal genes as characters and as many allelomorphs as deviations from the normal. In other words, as Russell remarks, the hypothesis crashes under its own weight. In his criticisms of this theory of the gene Russell merely wishes to draw attention to the fact that while the ‘genes’ have a certain heuristic value in reality they are purely hypothetical units.

He points out further that Mendelism applies only to sexual reproduction and because of sterility barriers the differences examined in genetical experiments are really unimportant to the normal form and its well being. When Mendelism is extended

<sup>1</sup> 1925, p. 187.

<sup>2</sup> 1930, particularly Chapters 5 and 14.

<sup>3</sup> 1930, p. 61.

*a priori* to cover cases of inheritance other than those studied in actual crosses, then a *petitio principii* is immediately introduced into the argument. For in such cases, and indeed in all cases, the assumption is made that paternal and maternal contributions to the zygote are of equal importance. Russell contends that this cannot be proved and in fact it is possible to construct a logical argument to the effect that inheritance of the chief characters might be purely maternal. "Now there is no means of telling, even by breeding experiments", says Russell,<sup>1</sup> "whether the general hereditary equipment comes from one parent only or from both. In intra-specific crosses all the main characters, those of the phylum, the class, the order, the genus, and the species, are common to both parents; what characters in the offspring can be definitely ascribed to one or other parent can only be those that distinguish one parent from the other, characters therefore of less than specific rank. In inter-specific crosses the differences may be larger, and the respective contributions may thus be more readily distinguishable, but even here the overwhelming majority of important characters are common to both parents. The fact that true crosses between quite diverse types are impossible to realize imposes of course a strict limit on this mode of analysis." Finally, as regards the theory of the gene, the only escape from difficulties of this kind lies in the hope that the genetic facts will sometime be re-interpreted in physiological or physico-chemical terms, not morphological. Russell himself, however, interprets genetics from the point of view of the organismal theory.

Russell further criticises the gene theory on the score of development. The facts of development indeed raise great difficulties for this theory because so very little is known about the effect of the genes in development. The theory of the gene is itself an extension of the theory of the germ plasm and so, from criticisms of the former theory, Russell passes on to criticisms of the latter more general one. This, of course, leads him to contrast the synthetic viewpoint of the organismal theory with the analytic viewpoint of the germ plasm and gene theories. The main argument of the organismal theory is that the "facts of development clearly show that the germ is primarily an organism, and only incidentally a cell. In fertilisation the egg cell is the only complete cell which takes part (for the male gamete in only the equivalent of the female nucleus). The stages of development indicate that the egg as an

<sup>1</sup> 1930, p. 270.



organism, i.e., as a unified cell working as a whole, plays the determining rôle. It is by a non-recognition of this point that the cellular conception of development fails."<sup>1</sup>

If this is so, then parts of cells cannot transmit the potentialities of the whole cell (in the sense of organism). The assumption that the chromosomes act in the metabolism of the cell enables the upholders of the organismal view to account for Mendelian inheritance without invoking the aid of genes or paricles of any kind, for slight modifications of the metabolism due to the chromosome would influence the organism as a whole, producing modifications of characters. And so Mendelian inheritance and chromosome behaviour are all "perfectly understandable on the view that the chromosomes normally play an important rôle in general metabolism. . . . But because rather definite and specific *differences* between individuals can be tracked down to *differences* between their chromosomes, it does not in the least follow that the chromosomes are the sole determiners of all the characters of the organism."<sup>2</sup>

<sup>1</sup> 1930, p. 265.

<sup>2</sup> 1930, p. 282. Sufficient account of Russell's important opinions has been given to enable the reader to understand the general position of "organicists" regarding heredity and development, but a complete account of the application of this point of view to general evolutionary theory still seems to be wanting.

## CHAPTER 9

### THE MODERN PERIOD CONTINUED :

#### (C) MODERN CAUSAL THEORIES OF EVOLUTION

##### 1. NEO-LAMARCKIAN IDEAS

###### (a) *General Account*

MANY causal theories of evolution have been put forward from time to time. Each of them has told us something about organic evolution but not one has been universally accepted. It is necessary, therefore, for us to consider the chief modern theories of evolutionary causation. We have already dealt with some of them, for it is not possible to give an historical account of the development of the evolution idea without bringing in the causal theories advanced in explanation of the processes involved. But in this chapter it is intended to deal with the more recent aspects of the various theories.

Conway Zirkle<sup>1</sup> in two papers in the *American Naturalist* gives an account of the views of those people who believed in the inheritance of acquired characters before Lamarck's time. He is most careful to point out (1) that a belief in this idea does not imply a belief in the evolution of species and (2) that for some 2,000 years before Lamarck's day practically all naturalists thought that acquired modifications were inherited. In his papers Zirkle then proceeds to give an account of the views of these earlier workers on this topic from the time of Hippocrates and Aristotle onwards. Zirkle's difficulty, in fact, was not to find writers who held to a Lamarckian view, but to discover any who did not believe in it. This belief, with one or two exceptions, was the accepted belief of the times and had no connection with the evolution concept. It was not thought that the hereditary acquirement of new characters led to the production of new species.

From the point of view of modern evolutionary ideas it is this belief in the inheritance of acquired characters which chiefly

<sup>1</sup> 1935 and 1936.

concerns us. With the remaining ideas of Lamarckism we are not concerned. To the modern Lamarckian, the organism strives to adapt itself to its environment; the results of this striving are passed on to subsequent generations until some obvious change or good comes from it. As F. B. Sumner<sup>1</sup> points out: "This is a valid scientific hypothesis with no necessary taint of mysticism about it. It is an explanation, moreover, which has much *prima facie* probability."

Neo-Lamarckians, then, have come to concentrate on this general controversial proposition of Lamarck respecting acquired characters. But, as a body of workers, experience has taught them to be tactful in stating their views. Thus it is really difficult to estimate what influence they have on present day biological evolutionary thought. Let us hear what H. S. Jennings,<sup>2</sup> a noted experimentalist and writer, has to say about it. He writes: "The commonplace assertion is that the inheritance of acquired characters is disproved; that no competent investigator harbours the doctrine: that the matter is out of court, no more to be considered. Yet the recent and present technical literature of zoology abounds in experimental investigations devoted to this question. Eminent authorities summing up the evidence affirmed that almost all experimentation directed on the matter supports the inheritance of acquired characters."

Soon after the period of the revival of Lamarckism, when Spencer, Packard, Cope and others were defending it against the Darwinians, some palæontologists had already come to the conclusion that neither natural selection nor the Lamarckian principle was the chief factor in evolution. Indeed, the realization of this conclusion led Osborn<sup>3</sup> to think that there must be some unknown factor in evolution. Later, Osborn developed this idea into his theory of aristogenesis, which we will consider later in this chapter.

Lamarckian experiments are usually most difficult to perform, take a long time to carry out, and require a special technique and a high degree of personal skill which is found in only few investigators. Thus confirmation of reported Lamarckian successes is rarely found. Further, in some cases, Darwinians maintain that the results of Lamarckian experiments may be interpreted in terms of artificial selection. The Lamarckian exposes an animal to some

<sup>1</sup> 1936, p. 436.

<sup>2</sup> 1930, p. 436.

<sup>3</sup> 1895.

stimulus and notes that it acquires a bodily modification. He then chooses or selects that animal and uses it as the starting point of his experiment. But selection in vigorously controlled populations is, in any case, limited in its effects. By the very nature of the experiment it is the subsequent behaviour of the organism which counts. To introduce the idea of selection in the sense of "choosing" but employ it in the sense of "natural" selection in the interpretation of Lamarckian experiments merely clouds the issue.

Robson and Richards,<sup>1</sup> in discussing this objection which is often brought by selectionists against the indirect evidence of the inheritance of acquired characters, have shown the limitations of selection and of the objection extremely well. They say: "A serious objection is brought forward by those who hold that in any particular case the correlation between the variation and the environment may be due to the selection of variants best suited to that environment. This objection is, quite literally, unanswerable, but it assumes what can never be proved, at any rate with our present knowledge. It is a very large assumption to maintain that a graded series of variations in a species corresponds to a parallel gradient of adaptations to the altering environment, if only because of the extraordinarily discriminative selection required. It appears to us that neither of these rival theories (i.e., Darwinism and Lamarckism) can be dismissed by a *a priori* argument. Both are possible, both are at present incapable of final proof and must in each case be judged by the balance of the evidence." For a true understanding of both Lamarckism and the selectionist experiments given in this and following chapter the points mentioned above should be borne in mind.

### (b) *Modern Evidence in support of Lamarckism*

#### (i) *General Account*<sup>2</sup>

A selection of the more modern experiments designed to show the inheritance of acquired characters will now be given.

<sup>1</sup> 1936, p. 55.

<sup>2</sup> Comprehensive accounts and arguments for and against Lamarckism up to about 1907 are given by Kellogg, up to 1925 by Detlefsen and up to 1936 by Robson and Richards, which work should be consulted by all those interested in this topic. Other accounts of Lamarckian experiments and reviews will also be found in the following: G. J. Romanes, 1895, Vol. 2; F. W. Hutton, 1899; H. Przibram, 1910; J. A. Thomson, 1910; R. Semon, 1912; P. Kammerer, 1924; J. T. Cunningham, 1928; and H. H. Newman, 1935.

The effects of use and disuse on organisms have long been known, for example blacksmiths, or those who constantly do heavy work, tend to develop large and hard muscles in the parts which are used, in contrast to office or sedentary workers, whose muscles are relatively small and soft. Lamarck indeed considered that the use or disuse of parts was responsible for evolutionary changes in animals. For this to be true, any changes induced by use or disuse must be inherited. It has proved to be very difficult indeed to show any case of the inheritance of changes due to such stimuli, or the lack of them. Inferential evidence of a kind has, however, been brought forward in this connection. We can mention the case of the callosities of the ostrich investigated and discussed by Duerden.<sup>1</sup> Or, again, in aquatic mammals the limbs and hip girdles are absent or only remain as vestiges. In the whale, for instance, the hip girdle is represented by a few apparently useless bones deeply sunken in the blubber; the whale also has no teeth but the embryos show the presence of bony structures in the jaws which are never cut. The suggestion in these cases is that these structures have degenerated through lack of use.

Again, Kammerer worked with *Proteus anguinus*, an amphibian which lives in water in underground caves in total darkness. The eyes of this animal are vestigial and are covered by skin. Hence they are blind; it is also colourless (except that the colour of the blood shows through the skin). Kammerer brought *Proteus anguinus* into daylight, whereon it became coloured brown and black, and this coloration was passed on to its progeny. He also kept the animals under conditions of alternating red light and daylight and found that the vestigial eyes developed normally. Many other cave animals are blind like *Proteus*, and also many deep sea fishes. The latter in fact often show many structural features which are regarded as adaptations to the special deep-sea environment. To Lamarckians examples such as these suggest that the changed surroundings have induced the changes in the animals. A selectionist interpretation is equally valid. Kammerer's evidence on *Proteus* suggested that an acquired character was inherited; on the other hand, a similar experiment by Payne gave a different result. This investigator<sup>2</sup> bred *Drosophila melanogaster* in total darkness for 69 generations without finding any change in the eyes or in their reaction to light.

<sup>1</sup>1920.

<sup>2</sup>1911.

However, it does not seem likely that experiments of this type will establish the truth or otherwise of Lamarckism. Lamarck conceived the animal as striving to better itself and its progeny. Striving creates habits; thus it is through interference with habits of animals that one may hope to demonstrate the inheritance of acquired characters. In a Royal Institution discourse delivered in 1931, MacBride, a leading British Lamarckian, who calls habit "the driving force of evolution", stoutly defended Lamarckism. He developed his thesis by showing that the real evidence for the occurrence of evolution is reducible in the final analysis to the habits of the animals which have evolved. He then proceeded to describe the most recent Lamarckian experiments on the inheritance of acquired habits (these are given below), and he concluded by explaining how acquired habits could be passed on to future generations. MacBride's discourse, which was published in *Nature*, provoked a spirited reply from J. B. S. Haldane which led to a controversy by these two men and Heslop Harrison. Anyone who wishes to know the modern position of Lamarckism should read this article and the letters to *Nature*.<sup>1</sup>

We may put forward MacBride's<sup>2</sup> views by the following quotation: "Briefly, then, my argument was this. Whenever we have evidence which enables us to determine with a probability amounting to practical certainty what the actual course of evolution has been, we find that it presents the same features, namely, an extremely slow and continuous change of structure correlated with a corresponding slow modification of habit. Since changed habits, by exercising different parts of the body, do modify structure, and since we know that animals can and do change their habits in response to the demands of a changed environment, it is a natural inference that the changed habits are the cause of the changed structure, and that the structural response on the individual has finally become engrained in the heredity of the race. So strong is the evidence for this inference, that some of my friends among the leading systematists of the British Museum deny altogether the necessity for direct experimental confirmation of it, arguing, with probable justice, that so many generations would be needed to make the change manifest that the time required would far exceed the span of an experimenter's life."

<sup>1</sup> MacBride, 1931, 1932a, 1932b; Haldane, 1932a, 1932b, 1932c; and Heslop Harrison, 1932.

<sup>2</sup> MacBride, 1932a, p. 900.

(ii) *Experimental Evidence in Multicellular Organisms*

Many experiments have been performed with a view to provide evidence for the proposition that acquired characters are inherited, and many of them have failed to do this; others have been suggestive, and some few seem to have given positive results. Even with this last type of experiment different biologists give diverse interpretations. Perhaps one may say that enough has been done to date to warrant the conclusion that the theory of Lamarck may yet prove to be one of the major theories accounting for the transformation of species. The experiments as a whole have shown that it would be rash indeed to brush them aside as of no significance.

We give below a sample of the more important and recent Lamarckian experiments; while in the appendix references to the older work and an account of some other experiments not included in the text are given. Most of these experiments have been described direct from the original papers, and enough detail has been given to enable the reader to form his own opinion about their significance and validity either for or against the Lamarckian idea.

(α) *P. Kammerer*<sup>1</sup>

In some of his experiments Kammerer investigated the effects of the colour of the environment on the skin colour of *Salamandra maculosa*.<sup>2</sup> There are two colour varieties of this species, in one (*forma typica*) yellow coloured patches on the skin are scattered over a black background, and in the other (*forma taeniata*) the yellow patches are longer and symmetrically arranged chiefly in two lateral lines on each side of the back. Kammerer placed specimens with very little yellow pigment in their skin on yellow loam soil with overhead illumination and kept them there for four years. He found that the specimens gradually became more yellow in colour but remained *forma typica* in pattern. When these animals were crossed among themselves the young produced were even yellower still, but in one specimen the pattern had become the pattern of *forma taeniata*. This result, and also the fact that when the artificial *taeniata* race was crossed with the natural *taeniata* race the progeny

<sup>1</sup> Many Papers and a general account of his work is given in *The Inheritance of Acquired Characters*, 1924. A good analysis of Kammerer's work is given by J. T. Cunningham, 1928.

<sup>2</sup> 1913.

were all *taeniata* in type, suggested to Cunningham<sup>1</sup> that whereas in some cases Kammerer was dealing with the somatic induction of characters, in this one case he was dealing with a case of parallel induction. Hence he considers that this result throws doubt on Kammerer's experiments. Harrison and Garrett,<sup>2</sup> however, in their important work on the induction of melanism in *Lepidoptera* point out that in experiments of this kind it is difficult to distinguish between somatic and parallel induction, for the germ cells must be influenced through the soma in any case.

When the yellowish specimens were reared in boxes with black garden soil and overhead illumination Kammerer found that they became progressively blacker in pigmentation. When these darker specimens were mated the offspring were so black as to be almost indistinguishable from *Salamandra atra* (the black salamander). Further, Kammerer also found that when the young yellow progeny from the yellow boxes were placed in boxes with black soil, the amount of yellow pigment in their skin increased for the first few months, thus showing that the acquired yellowness effect was inherited in spite of the changed external background colour, but after six months the influence of this dark coloured background began to tell, as expected.

We may conclude this of Kammerer's work by quoting MacBride<sup>3</sup> who says: "We may sum up Kammerer's results thus. The animal responds to a change in environment by an alteration in the proportions of its pigment: this response produces an effect on the offspring so that they tend to start where their parents left off; if they continue to live under the same conditions as did their parents the effect of the environment is intensified; if they are exposed to different conditions, then the effect of the experience of the parents still shows itself during the early period of their life: in a word, the young recapitulate the response which the parents had learned to make." Kammerer himself considered that these coloration experiments, while showing Lamarckian effects, also showed that the type *taeniata* was produced, or evolved, from the type *typica* by the action of the colour of the natural environment.

Kammerer, by altering the habits of the European Salamander also succeeded in altering several specific habits relating to reproduction of their young. In *Salamandra maculosa* about 20

<sup>1</sup> 1928, p. 135.

<sup>2</sup> 1926, p. 261.

<sup>3</sup> In *Evolution in the Light of Modern Knowledge*, ed. 1932c, p. 241.



young are born as aquatic larvæ with gills (or eggs are shed which hatch immediately). The gills gradually disappear and eventually the adult land salamanders are produced. In mountainous regions, however, the young are born with smaller gills and also four legs. On the other hand, *S. atra*, which normally lives in mountainous regions, is normally viviparous and produces two young salamanders at birth; there is no aquatic stage.

Kammerer reversed the habits of these animals and found that when *S. atra* was kept under moister and warmer conditions the number of young it produced increased year by year, and they were aquatic, like the larvæ of *S. maculosa*. On the other hand, when *S. maculosa* was kept under dry and cool conditions fewer and fewer young were produced each year, and furthermore in each successive year their gills showed a diminution in size, until in the end completely formed terrestrial salamanders were produced. The fact that the changes which took place in the reproductive features of these animals were only induced gradually indicates that the new acquired habit (brought about by changed conditions) was inherited and hence that a Lamarckian effect was produced.

(β) *J. W. Heslop Harrison on the Egg-laying Instincts of the Sawfly*

Heslop Harrison's<sup>1</sup> well-known investigation of the feeding instincts of a sawfly, besides providing evidence for Lamarckism, is of the greatest value, firstly, because it concerns the naturally-induced change of a fundamental instinct without applying an artificial stimulus, and secondly, because the experiments were carried out under purely natural conditions in a garden. Hence a rather full account of the work is given.

*Pontania salicis* feeds on various species of willow, but each individual colony prefers its own special species of willow, on which the eggs are deposited, and on which the larvæ feed. Heslop Harrison attacked this problem in two ways, which he described as follows:—<sup>2</sup>

(1) "Attempts could be made, by removing a strain of the insect chosen for the work from the plant to which it has been accustomed, to a habitat in which a wholly different species of *Salix* grew, to compel it to take to that species. If it proved wholly

<sup>1</sup> 1927.

<sup>2</sup> 1927, p. 117.

or partially acceptable, the new colony could be allowed to develop on it for some years. At the end of that stage the heritability of the new food habit could be tested by giving the insect access once more to its original food plant."

(2) "In much the same way, a strain could be taken to a station in which many species of *Salix*, including its own normal food plant, were available for oviposition. By direct observation of the species upon which gall development took place deductions immediately applicable to the solution of the problem in hand could be made."

In his first experiment Heslop Harrison took galls of *Pontania salicis* from two different localities and allowed the emerging sawflies perfectly free access to a garden containing many species of willow, besides other shrubs. For three years gall counts were made. It was found (a) that the original strain from *Salix purpurea* produced galls only on *S. purpurea*, and (b) that practically all of the descendants of the original strain from *S. phylicifolia* produced galls on *S. Andersoniana* and *S. phylicifolia*. These two species are so closely related as to be considered one species by some systematists, but they differ in chromosome number.<sup>1</sup> Some galls were found on *S. rubra* which is a hybrid between *S. purpurea* and *S. viminalis*, but they all aborted except in the third year, when seven of them persisted. The *phylicifolia* strain of *Pontania* showed a great and increasing preference for *S. Andersoniana* to the comparative neglect of *S. phylicifolia*.

Heslop Harrison considered that perhaps this was an inherited preference and so it was tested by giving the insects free access to *S. phylicifolia*, but restricted access to *S. Andersoniana*; subsequently galls were found only on the latter. The inference drawn from these experiments was that the strain of *Pontania salicis* concerned confines its effective feeding to *Salix Andersoniana* (and *S. phylicifolia*) and that this feeding habit became germinally fixed.

In the next experiment Heslop Harrison took galls of a *Salix Andersoniana* feeding strain of *Pontania* and transferred them to a plot where only the rare hybrid *S. rubra* grew. In the first year galls were formed, but most of them aborted. In the next year new *Andersoniana* sawflies were introduced; gall formation started, but still most of them aborted. In the next year the number of healthy galls was found to be increased and the colony was established. Nearly two years later six plants of *S. Andersoniana* were planted in the plot. During the two following years when ex-

<sup>1</sup> Blackburn, K. B., and Heslop Harrison, J. W., 1924.

amination was made the colony was seen to be flourishing, and galls were only found on *S. rubra*, with none at all on the original food plant *S. Andersoniana*. This means that the newly acquired habit of oviposition on *S. rubra* had been germinally fixed, demonstrating, as Heslop Harrison says:—"An incontrovertible case of the inheritance of acquired characters."<sup>1</sup>

In 1931, E. W. MacBride restated the case for Lamarckism in a discourse which was printed in *Nature*, giving Heslop Harrison's work with *Pontania* as one of the more important pieces of evidence. In the following year J. B. S. Haldane<sup>2</sup> replied, disagreeing with both Heslop Harrison's and MacBride's interpretations of these *Pontania* experiments. He noticed that in the first two years of the experiments described above all the galls on *Salix rubra* aborted, but in the third year seven survived. In the next experiment, during the first two years many, but not all, of the galls on this plant aborted, while in the third year the colony was fully established. Hence Haldane inferred that those insects which showed a preference for *S. rubra* were selected, the rest perished, or that, as MacBride points out,<sup>3</sup> the strain of sawflies had become contaminated with one which preferred the *Salix rubra* hybrid, and that these were the ones which survived. In the first case, however, Haldane has overlooked Heslop Harrison's safeguard, in which he showed that all the insects originally preferred *S. Andersoniana* to the exclusion of all others, which were easier to reach.<sup>4</sup> While in the second case MacBride replied by pointing out that *S. rubra* is a rare hybrid, and so it is fantastic to imagine that the strain of *Pontania* from *S. Andersoniana* had become genetically mixed up with a strain from such a rare plant just at the time that Heslop Harrison began to use it. Indeed, if such occurred, it would be more than a coincidence. Earlier, MacBride<sup>5</sup> had rebuked Haldane for invoking selection in this case by writing: "Selection as an effective cause of anything is a superstition which dies hard. That some animals live and some die is known to everyone, but unless the some that die differ from those that live no change is produced."

Haldane, following Wheeler, further suggested that the adult insects lay their eggs on the first food plant by choice determined by larval memory. This idea may seem to be rather far-fetched,

<sup>1</sup> 1927, p. 123.

<sup>2</sup> 1932a, 817-819 and 856-858.

<sup>3</sup> *Nature*, 1932, p. 128.

<sup>4</sup> Harrison, 1927, p. 120.

<sup>5</sup> 1932, p. 900.

but Wheeler<sup>1</sup> has pointed out that the central nervous system is practically the sole larval system which is not changed during metamorphosis. It may then provide a mechanism for carrying over a larval state. In any case, if such a mechanism operates, one wonders why the insects in Heslop Harrison's experiments laid their eggs at all on any other plant but the original one, or if it was not present in the immediate locality, why did they not attempt to find it? To try to force an explanation of an experiment other than the obvious one, as Haldane does in this case, by invoking some mechanism about which little, if anything, is known, rather weakens the case for anti-Lamarckians.

Another selectionist, J. S. Huxley, attempts to interpret this work in terms of organic selection. According to Huxley, in organic selection a modification which is repeated for a while in an organism may take a part in evolution by holding the strain in a favoured environment so that the mutation which produced the modification has a chance of becoming fixed in the genetic constitution of the organism. As Huxley<sup>2</sup> says: "The process simulates Lamarckism but actually consists in the replacement of modifications by mutations." Huxley considers that in Heslop Harrison's work the high mortality of the galls on *S. rubra* indicates that he was dealing with mutations and not acquired characters. These mutations were then organically selected. The Lamarckian effect was merely simulated. Experimentally, it has been shown that mutations arise at random. But somehow or other selectionists manage to find them arising at the correct moment when dealing with experiments which are designedly anti-selectionist. Again, one may ask how did a race attached to *Salix Andersoniana* carry latent tendencies to oviposit on *S. rubra*, and manage to maintain such hereditary possibilities? And how did they arise in any case, for the contact between *S. phylicifolia* and *S. Andersoniana* on the one hand and *S. rubra* on the other is negligible?

#### (γ) William McDougall's Lamarckian Experiment

In 1920, William McDougall, a psychologist, began what must be one of the most elaborate biological experiments yet devised; he finished it in 1937. The four papers<sup>3</sup> embodying the results of

<sup>1</sup> 1923, p. 51.

<sup>2</sup> 1942, p. 304.

<sup>3</sup> 1927, 1930, 1933 (under Rhine and McDougall), and 1937.

the experiment (or series of experiments) are surely models of their kind and must rank among the classics of scientific literature. The author considers the question whether acquired characters are inherited or not to be of far-reaching importance for biology, psychology and sociology generally, because on it depends our approach to the question of "mind versus matter". If Lamarckism is true, then, according to McDougall, the edifice of Mechanism with all its materialistic implications falls to the ground. McDougall<sup>1</sup> puts forward his reason for carrying out an elaborate experiment of this kind in the following words:—"If the Lamarckian hypothesis be valid, if it be true that modifications of function and structure, acquired by the individual organism in consequence of its efforts to adapt itself to its environment, may be in some degree, however slight, transmitted to its descendants, then we have in outline an adequate theory of organic evolution; and, further, we are able to assign to mind, or, in other words, to purposive, teleological or hormic activity, an intelligible and leading rôle in the drama. On the other hand, if we can find no warrant for accepting the Lamarckian hypothesis, then we remain utterly in the dark as to the nature of the evolutionary process; we have no theory of it, and the place of mind in the scheme remains utterly unintelligible. For it is now generally admitted that the Darwinian principle of natural selection (including under that term all varieties of selection, organic, sexual, social, germinal, etc.) does not give us a tenable theory of evolution, so long as we postulate only fluctuating variations or indeterminate mutations." We have tried to show in a preceding chapter that the popularity of the selection theory in evolution is due in some measure to the rise of mechanistic ideas in biology, and of materialistic ideas generally at about the time when Darwin first promulgated his theory.

The recognition by McDougall of the fundamental antagonism between Lamarckism and selectionism undoubtedly led him to present his results and conclusions in a model way. He considers his problems from all angles, he points out all the difficulties and minimises none of them; he gives a detailed description of procedure and methods used in the experiments and of all subsequent modifications. He also discusses the effects of the experimental conditions of his animals; he anticipates criticisms; and, as we have already indicated, what is most important of all, he analyses his probable

<sup>1</sup> 1927, p. 268.

bias and the steps taken to prevent it from affecting his results. He<sup>1</sup> can say with all truth: "I am well aware of the possibilities of many subtle flaws in my procedures and of subtle errors in the reasoning process. Hitherto I have failed to discover such flaws or errors; . . . . ."

Like Heslop Harrison when he worked on *Pontania*, McDougall realised that the first requirement of a Lamarckian experiment should be one which aspired to help the animals used to adapt themselves to a new condition through the exercise of their own "intelligent" effort in as natural a way as possible. He also considered it important that the animal chosen for the experiment should belong to a quick-breeding kind and that the work should be carried on for a long time.

McDougall worked with a stock of pure-bred white rats which he divided into two lots. One lot was used in a water-maze experiment, and the other in a water-tank experiment. In both experiments after thirteen generations of rats had been tested evidence of increasing ability in leaving the tanks was indicated. But for several reasons the water-maze experiment was discontinued and attention was henceforth confined to the water-tank experiment. While testing the behaviour of the rats up to the thirteenth generation several unforeseen flaws were found in the water-tank used in the experiment and in the procedure adopted. These were all corrected. So that up to the thirteenth generation the results were merely suggestive, but after this they were more truly significant and amenable to interpretation.

The tank used in the experiment was divided into three compartments (B, O, and A, see fig. 6) by two partitions. Of these, the middle one was blind at one end but at the other end it communicated with the compartments on each side. The two lateral compartments led to a platform (P) and freedom. The tank contained water to the depth of 6 inches. At the end of each lateral compartment a piece of frosted glass was placed at a certain height and beyond was a light which illuminated the passage at that side. An electric device was arranged so that if necessary a shock could be given to a rat as it emerged from the water and stepped on to the dry platform.

Each rat was given a chance to become accustomed to the tank before actual training was commenced. For this the rat was taken when it was between 21-28 days old and lowered, head down,

<sup>1</sup> 1927, p. 272.

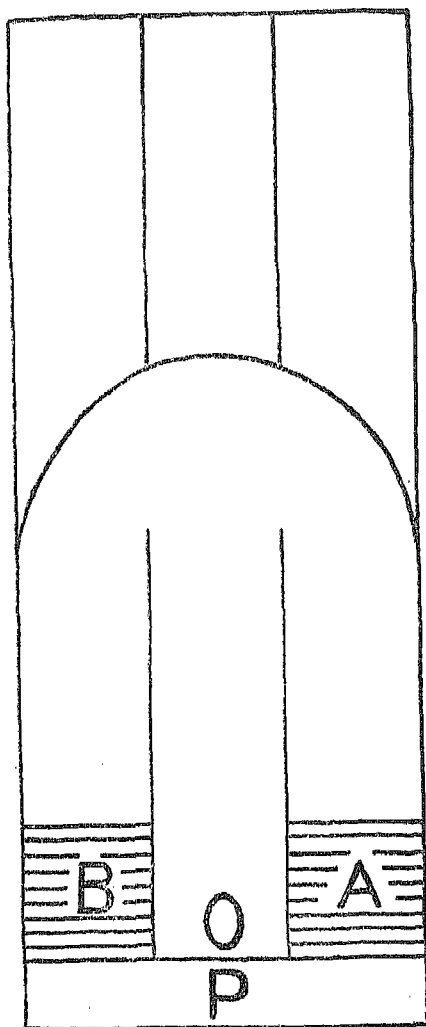


Figure 6. Legend

The figure represents the modified form of tank as used by McDougall in his experiments with rats. *O* represents the passage way into which the rat was placed, the only exit being the distal end leading to the sloped passages *A* and *B*. The tank was half filled with water so that a platform *P* placed just above the water level provided the only means of escape from the tank. (Alter Rhine and McDougall, *Brit. J. Psych.*, 24, p. 213. 1933-4.) For further explanation, see text.

into the centre compartment at the point O. This procedure was repeated for six times at minute intervals, and on each occasion the lateral compartments were illuminated and dimmed alternately. McDougall refers to the first day of the experiment as "zero day". On the second day the training began, and on this day and every succeeding day until the rat was fully trained the same procedure was followed, only now the compartment which was lit was also electrified so that if the rat chose this compartment in order to escape it would receive a shock as it climbed on to the platform. Each rat was immersed six times each day during training. If it swam down the bright passage it would receive a shock on the platform, but if it swam down the dim passage it would escape without receiving a shock. When the rat learnt to avoid the lit and electrified passage twelve times in succession it was considered that the training was completed. The trained rat, as McDougall puts it, is one which "learns to discriminate between the bright and the dim gangway (in anthropomorphic terms it learns to accept the bright light as a signal warning it of a shock)."

The important feature of this experiment is that by means of the tank procedure each rat is forced to make a choice discovered by means of trial and error between two passages. To make this choice involves the association of ideas in the rat of coupling a bright light with a shock and a dim light with no shock. The task was difficult (in some cases it took 330 or so immersions before a rat learned the lesson it was meant to), and the process of learning was sufficiently laborious to warrant the assumption that perhaps the training would impress itself upon the constitution of the animal sufficiently to influence succeeding generations in their choice of pathways, or at least in the time taken to learn to distinguish between the two pathways. In other words, McDougall attempted to develop a certain inherited habit in the rats.

Table 2 reproduces McDougall's table 7 of his fourth paper (1937) which summarises the results of his main experiment. In this table T.R. represents tank rat.

This table shows quite clearly a persistent falling off in the average number of errors per rat as we proceed from the 13th or 14th generation to the 43rd or 44th generation. McDougall claims this falling off means that, whatever the actual mechanism causing it, the rats of later generations learnt more quickly than those of earlier generations, and as the training was the same in all rats it seems to show that the rats of succeeding generations have inherited



an "experience" gained by those of the former generations. McDougall was careful to point out that additional evidence for this inheritance of learning was given by the figures of the zero-day

Table 2<sup>1</sup>

*The General Course and Effects of Training of Rats prolonged through many generations.*

Generation of T.R. stock	Number of rats	Average number of errors of errors per rat	Number of errors made by		Zero-day choices
			Best rat	Worst rat	
13	23	68+	30(1)	90+	76 - 62
14	10	80	42(1)	102	31 - 29
15	10	70	39(1)	96	24 - 36
16	5	73	39(1)	88	14 - 16
17	11	46	9(1)	147	35 - 31
18	22	62	15(1)	142	59 - 73
19	15	47	12(1)	100	44 - 46
21	34	37	9(3)	74	91 - 113
22	16	36	6(3)	89	51 - 45
23	26	25	3(2)	71	73 - 83
24	14	33	10(1)	62	43 - 36
25	18	38	14(1)	78	51 - 57
26	23	43	9(1)	75	65 - 73
27	32	54	12(1)	96	98 - 94
28	17	44	19(1)	90	51 - 51
29	20	50	18(1)	105	51 - 69
30	11	20	3(2)	58	28 - 38
31	38	40	3(2)	100	115 - 113
32	42	17	3(5)	70	137 - 115
33	24	33	2(3)	73	93 - 51
34	34	36	2(3)	88	123 - 81
35	29	36	0(2)	124	89 - 85
36	24	28	2(4)	89	96 - 48
37	16	13.5	0(3)	65	64 - 32
38	21	8	1(10)	25	87 - 39
39	34	14	0(8)	50	130 - 74
40	15	29	0(2)	87	57 - 33
41	30	35	6(1)	78	93 - 87
42	27	23	1(2)	59	94 - 68
43	29	20	0(3)	52	100 - 74
44	30	9	0(11)	32	115 - 65

choice shown in the last column. This evidence first became apparent in the 32nd generation.

As we pass down the generations we see evidence of an increasing preference for the dim passage, or an increasing aversion for the light

<sup>1</sup> From McDougall, *Brit. Journ. Psych.*, 28, p. 323, 1937.

one. The zero-day figures give the behaviour of the rats on the day preceding the first training day, i.e., on the day when the rats were being familiarised with the tank and the passages in the absence of the electric shock. When these generations are put together in groups of 8 each, the points already stated are even more vividly brought out.

In another series of experiments, McDougall<sup>1</sup> trained a set of rats and from among them chose those which made the greatest number of errors and used them for breeding the next generation. This was repeated for 24 generations. In spite of this continuous adverse selection, the results showed an increase in learning facility only slightly behind that of the corresponding generation of the randomly selected rats, indicating that selection had only played a small part in the main experiments.<sup>2</sup> T. M. Sonneborn<sup>3</sup> had previously criticised McDougall's earlier experiments on the score of selection, but remarked: "As he (i.e., McDougall) justly feels, a marked increase in facility in successive generations even against unfavourable selection will be strong evidence for his claims of Lamarckian selection." In these later experiments, McDougall has shown just this "marked increase in facility . . . against strongly adverse selection".

McDougall also performed two similar experiments using favourably selected rats, i.e., rats showing the best behaviour used for breeding for the next generation. In the first case, only 7 generations were obtained before the strain became sterile. In the second case the experiment was carried on for 10 generations. The results indicate quite distinctly that the best rats have little advantage over the worst ones in acquiring the habit of avoiding the brightly lit passage.

In another experiment, three slow females of one lot of rats which made about 215 errors were mated with three males of another batch which made about 40 errors. The  $F_1$  showed an average error of 62, and when these were inbred and the  $F_2$  rats tested, the average error was about 64<sup>4</sup>. Later,<sup>5</sup> similar experiments were performed with similar results; in one case he used a hooded female mated to a male which made no errors. McDougall himself

<sup>1</sup> Papers 2, 3 and 4, 1930, 1933, 1937.

<sup>2</sup> In this experiment the average number of errors per rat dropped more or less consistently from 215 in the 3rd generation of adversely selected rats to 27 in the 24th generation.

<sup>3</sup> 1931, p. 549.

<sup>4</sup> See Paper 2, 1930.

<sup>5</sup> See Paper 4, 1937.

considers that these cross-breeding experiments show that the facility for learning is inherited in a definite fashion through the germ cells, and that the germ cells of a good father have a decided effect on the behaviour of his progeny. The experiments also dispose of such criticisms as that which maintain that the mother may influence the behaviour of her young either before or after birth, or that the differences of learning ability are due to accident and not to innate or inherited causes, etc.<sup>1</sup>

McDougall's Lamarckian experiments have been subjected to criticisms by F. A. E. Crew and T. M. Sonneborn (1931), W. E. Agar (1935), Thorpe (1939) and others. McDougall, however, has been able to give full replies to them. One feature of the controversy which he began stands out: McDougall presented his work in full detail, and as they stand his results justify his conclusions, yet in many textbooks, while his work is mentioned, it is rarely described sufficiently to allow the reader to judge the facts for himself. The true situation seems to be one of *ad hoc sub judice lis est*, with the weight of evidence strongly in McDougall's favour.

F. A. E. Crew repeated McDougall's experiment, but did not obtain any evidence of Lamarckian transmission. With the humility of the man who knows his own strength, McDougall acknowledges that if he is unable to explain the differences between his own results and those of Crew, then he has no case to answer. McDougall, however, does explain the differences between his own and Crew's results so competently as to reduce the significance of Crew's results in relation to his own practically to zero. He points out that, whereas Crew used a similar tank and methods of work to his own, the differences between their actual procedures were so great as to render comparisons between the results of the two sets of experiments unsafe.<sup>2</sup> The difference between

<sup>1</sup> In a discussion on McDougall's first two papers, F. A. E. Crew had suggested that the mother of a litter of rats may somehow influence the behaviour of her family (see *Eugenics Review*, 1930).

<sup>2</sup> Crew's method was as follows: In the earlier generations he gave each rat 6 trials with the light alternating in each passage just as did McDougall, and then in the later generations he changed his procedure by dividing the training period into three phases as follows: (a) each rat was given 50 trial runs with equal light in both passages and no electric current, (b) this was followed by another 50 trials with the light alternating in the passages but no current, and (c) this was followed by the actual training period with one passage both illuminated and electrified. Crew carried his work to 18 generations (so as to compare with the first 21 of McDougall's), and he used a much larger number of animals for the tests in each generation. He also used a larger number of control animals.

the two sets of experiments is shown in detail in his fourth paper.<sup>1</sup>

McDougall points out that Crew's results show that his rats were offered a very much easier task to perform than McDougall's. In some cases, Crew's rats required no training, in others very little training. McDougall<sup>2</sup> remarks: "It is obvious that in so far as the purpose of the procedure is to bring to light any transmitted effect of training in successive generations, a form of procedure which omits all training from some members of each generation and gives to many others only a very slight training is *ipso facto* disqualified to throw light upon the problem in hand." It is probable that the more difficult the task, i.e., the longer the rats have to be trained, especially in the first few generations, the more will the training become impressed on each rat. If there is any such thing as inheritance, it is reasonable to assume that the rats must be given the chance to learn. There was a very great difference in the lighting arrangements in the two tanks used by these workers, and McDougall is inclined to think that this difference may be the reason for the easier task of Crew's rats.

Again, McDougall<sup>3</sup> points out that Crew's results show great variations in the average score of 18 control groups, which suggested to McDougall that Crew's technique involved a large experimental error which was absent in McDougall's technique. Such a wide experimental error would tend to obscure the results by masking the legitimate variations of improvement of learning facility. McDougall began to train his rats when they were 21-28 days old, while Crew did not do this until his were 75 days old. Crew himself points out that this age difference must be taken into account when comparisons are made between their results. He thinks, however, that it makes no essential difference.<sup>4</sup> On the other hand, McDougall considers that this difference in procedure is very important, for it would seem that young animals are more susceptible to training than older ones, as we know from our own experience. Indeed, if this is so, we might expect that Crew's more staid and fixed rats would show little, if any, innate response to training.

In criticism of McDougall's experiment, Crew suggests that the inherited facility for learning which is undoubtedly shown by the

<sup>1</sup> 1937, pp. 335-345.

<sup>2</sup> 1937, p. 338.

<sup>3</sup> 1937, pp. 338-345.

<sup>4</sup> 1936, p. 66.

former's figures is possibly due to some "genetic accident", whereby a few of the males which are used in breeding the later generations carry a hidden gene for quickness in learning. This gene is regarded as normally dominant, but for some reason or other it may not always express itself. Thus, we may have a slow rat which is potentially a quick one in which the gene for quickness is awaiting the chance, as it were, to start work. This criticism will be familiar to geneticists, for its use enables them to cover up a multitude of difficulties, but in this case, as McDougall points out, the argument is built up on a mass of successive suppositions. With each successive generation of rats the case for this criticism weakens. Crew is inclined to think that the gene produces a photo-phobia in the rats, but there is no evidence to show that the character of photo-phobia in the rats is either a definite clear-cut one, or is inherited in a Mendelian fashion.

Both Crew and McDougall found that rats with good general vigour learn to avoid the electric shock slower than rats of rather less than average vigour. From this, Crew suggested that the increased learning of McDougall's rats, generation by generation, could be accounted for by a steady deterioration of physical constitution. McDougall, however, replied by stating that, while certain odd generations had shown a decreased vigour there was no consistent deterioration; in fact, some of the rats of the later generations were exceedingly vigorous.

Again, Crew criticises McDougall's experiments on adverse selection of the rats, but he does so on the basis that quickness and slowness in rats is controlled by a gene and inherited in some sort of Mendelian way. But there is no evidence to support this contention, and the point to notice is that in McDougall's experiments, in spite of continuous adverse selection, the rats learnt so quickly as to exclude the possible effects of any effective selection.

T. M. Sonneborn,<sup>1</sup> in a very fair account of McDougall's first two papers, criticised the experiments on the score of inadvertent selection. McDougall is said to have chosen his rats at random by taking the first two animals that came to hand when the door of the cage was opened. Sonneborn points out that, according to a well-known breeder of guinea pigs, the active and clever ones rush to the door when it is opened, which suggested that McDougall was in fact choosing the best rats all the time. If this is so, since McDougall has shown that the most vigorous

<sup>1</sup> 1931, p. 547.

animals rush to the bright passage and so receive more shocks than the less vigorous ones, McDougall's figures are even more striking.

( $\delta$ ) *D. E. Sladden and H. R. Hewer on Carausius*

The most recent Lamarckian experiment is that of Miss Sladden and H. R. Hewer,<sup>1</sup> who studied the inheritance of an induced food habit through six generations of a stick insect called *Carausius morosus*. This insect is parthenogenetic for long periods; males only appear rarely. Hundreds of insects of known parentage and food habits were tested in two ways by means of (a) presentation tests and (b) preference tests. In the former, the insects were given ivy and privet (the normal food) alternately until they accepted the ivy. They were then grouped according to the number of presentations made (i.e., according to the number of times the ivy was presented until it was accepted by the insect) in each generation. In the preference tests, both privet and ivy were given on each of three successive feeds, and three classes of insects were noted: (a) those that took only ivy, (b) those that took only privet, and (c) those that took both ivy and privet. The controls and the ivy-fed insects were submitted to both of these tests.

As large numbers of these parthenogenetic insects were dealt with, and as the selection of eggs was purely random, the usual criticism of experiments of this type cannot be levelled at this one. Even such a staunch selectionist as J. S. Huxley<sup>2</sup> admits this. The results were checked by means of reversal tests and periodicity tests, and by the effects of feeding the insects on other foods, and in view of these checks the results seem to provide evidence in favour of the Lamarckian idea.

Sladden and Hewer's tables of results (two of which are reproduced below; see tables 3 and 4) show that the experimental insects (i.e., those fed on ivy continuously after this habit was induced in them) display an increasing ability to accept ivy as food with each succeeding generation; while for the first four generations the control insects (i.e., those fed on privet in each generation but tested for ability to take ivy) also showed an increasing ability to accept ivy as food, but in a much less degree than the experimental broods; in the fifth and sixth generations, however, these controls showed a decreasing ability to take ivy.

<sup>1</sup> 1934, 1935 and 1938.

<sup>2</sup> 1942, footnote, p. 303.

Further analysis of the results showed that the ability of the privet-fed insects to take ivy is a function of the season of the year when the food is presented, i.e., there is a periodicity in the feeding habit, but this does not apply to those insects in which ivy-feeding had been induced. Summing up, Hewer writes: "It is difficult to escape the conclusion that the forced ivy-feeding has induced the increased ability to accept ivy in each succeeding generation in this parthenogenetic insect."<sup>1</sup>

*Table 3<sup>2</sup>*  
*Summary of Presentation Tests.*

Duration of experiment	Filial generation	Privet-fed parents. Presentation of ivy									
		1	2	3	4	5	6	7	8	9	10
Jan.-April	1	8.0	32.0	21.6	12.0	11.2	11.2	2.4	0.8	0.0	0.8
Nov.-Jan.	2	30.7	46.0	14.7	2.0	3.3	0.7	0.0	0.0	0.7	—
Nov.-July	3	54.2	40.9	4.8	0.0	0.2	—	—	—	—	—
Sept.-Nov.	4	61.0	39.0	—	—	—	—	—	—	—	—
Mar.-Aug.	5	58.8	34.8	5.0	1.2	0.2	—	—	—	—	—
June-Aug.	6	86.0	13.6	0.3	—	—	—	—	—	—	—

		Ivy-fed parents. Presentation of ivy									
		1	2	3	4	5	6	7	8	9	10
	1	—	—	—	—	—	—	—	—	—	—
Oct.-April	2	78.25	18.99	1.5	0.12	0.12	—	—	—	—	—
Aug.-May	3	93.7	6.2	0.1	—	—	—	—	—	—	—
July-Feb.	4	90.3	9.5	0.3	—	—	—	—	—	—	—
Aug. . .	5	100.0	—	—	—	—	—	—	—	—	—
July-Sept.	6	82.0	17.5	—	—	—	—	—	—	—	—

*Table 4<sup>3</sup>*  
*Summary of Presentation Tests*

Filial generation	Privet-fed parents			Ivy-fed parents		
	privet	neutral	ivy	privet	neutral	ivy
2	44.0	35.0	21.0	28.2	37.0	35.6
3	33.2	44.0	22.8	16.5	39.9	43.4
4	26.0	46.0	28.0	14.0	39.0	47.0
5	22.0	36.0	42.0	2.0	54.0	44.0
6	10.0	54.0	36.0	6.0	36.0	57.0

<sup>1</sup> 1938, p. 44.

<sup>2</sup> From Sladden and Hewer, 1938, Table 6, p. 35.

<sup>3</sup> *ibid.*,

(iii) *Experimental Evidence in Unicellular Organisms*

No account of Lamarckian effects would be complete if it ignored the evidence provided by unicellular organisms.<sup>1</sup>

Many *protozoa* like *Paramecium*, the slipper-animalcule, can be altered in form and in their physiological states by placing them in new environments, produced by adding various chemicals to the water in which they live, or by raising the temperature. On restoring the animals, or their descendants, to the original surroundings, the modifications usually disappear. But not all environmentally induced changes in these organisms are of this kind, for some are definitely inherited. For example, if some *protozoa* are kept under bad conditions their descendants for many generations may reflect the conditions in such things as reduced vigour, slow metabolism, etc. If kept in very good conditions the descendants may show good effects. If subjected for many generations to gradually increasing temperatures these animals may develop resistance to very high temperatures. For instance, by gradually increasing the temperature over a period of seven years Dallingier and Drysdale<sup>2</sup> enabled several *Infusoria* to survive in a temperature of 70° C. whereas the normal one in which the animals live is about 25° C. Treatment with chemicals such as arsenic, antimony, calcium induces changes. The acquired character is furthermore seen to be specific in that each chemical produces one type of change. Neuschloss obtained evidence that such induced changes may be due to altered metabolism. Changes in resistance, or metabolism, such as these may be inherited for hundreds of generations after the organism concerned has been transferred back to normal conditions. They may then gradually decrease until finally they disappear.

The length of time an agent acts on the unicellular organism seems to have an effect. Jollos,<sup>3</sup> working on *Arcella*, found that the longer an agent acts, the longer it takes for the induced and inherited

<sup>1</sup> An excellent account of the inheritance of acquired modifications in unicellular organisms is given by H. S. Jennings in his *Genetic Variations in Relation to Evolution* (1935, Chap. 4 and 5). The account in the text has been partly taken from this book, and from the papers which Jennings gives in his bibliography. Some general references to Lamarckian work on unicellular organisms are given: on *protozoa* and on genetics—Jennings, 1906, 1929, 1935; Sonneborn and Lynch, 1934; Jollos, 1920; on parasitic *protozoa*—Taliafera, 1926 and 1929; on bacteria—Manwaring, 1934; Philip and Hadley, 1927.

<sup>2</sup> See Jennings, 1935, p. 106.

<sup>3</sup> 1920.



modification to disappear. Jollos considers that the environmentally affected genic materials lie in the cytoplasm, or the macronucleus of the cell, but not in the real or micronucleus. He calls this phenomenon *Dauermodifikation*. Such acquirements do not change the animal's potentialities, they only prevent them from being expressed for a time. Jennings, however, points out that many modifications which ultimately disappear may yet persist long after any effects from the original cytoplasm or the original macronucleus could possibly act. This latter type of change could be passed on from generation to generation by the micronucleus. Finally, the question arises: "How are the modifications actually brought about?" And while there is no answer to this question, Jennings considers that inherited modifications which are also adaptive are due to some kind of selection within the cell or tissues of the organism.

## 2. BIOMECHANICAL EVOLUTION FORMULATED THROUGH ORTHOGENETIC PHENOMENA : ARISTOGENESIS

Straight-line evolution, or the idea of definite trends or directions in evolution, has long been recognised, and is now an accepted evolutionary theory (see page 166). Most of the evidence for orthogenesis is provided by the palæontologists, who have unearthed many series of animals which show a form of development resembling the unrolling of a pattern. Orthogenesis is the evolution of groups of organisms along parallel lines. Many of these lines are still in existence and they stretch back into the unmeasurable geological past. Others have become extinct, but the pattern which they show often betrays the causes of their extinction. For example, in the case of a certain mollusc, the geological strata show how it gradually evolved by some slow and continuous process to become the marine organism called *Gryphaea* which eventually died out during the age of the chalk beds. As this mollusc evolved, its shell gradually became more and more coiled until finally the animal could scarcely open it, and so the animal perished. Other examples of such orthogenetic series described in textbooks are the ammonites, the extinct Titanotheres, which were very large mammals, the elephants and the horses.

The point we wish to emphasise here is that many of the orthogenetic series shown among the fossils are difficult to explain

from a Darwinian point of view. In fact, many orthogeneticists are anti-Darwinians, but there are two schools of thought among them. Some orthogeneticists hold the view that straight-line evolution is due to an inner directing force or agency which is inherent in the germ plasm and propels the species along its pre-determined path. Nägeli held ideas of this nature, and Berg believed that the extinction of animals is due partly to internal causes. Other orthogeneticists, disliking the idea of an intangible inner urge, sought a causo-mechanical explanation of straight-line evolution by appealing to Lamarckism. These palæontologists may therefore be called neo-Lamarckians. As representing the advanced views of modern orthogenetic theory, we may now deal with Osborn's idea of what he calls "bio-mechanical evolution", which includes within it the concept of *aristogenesis* as the causal principle. Osborn, in fact, was one of the foremost palæontologists and has probably written more on this subject than any other modern writer.<sup>1</sup>

Before the end of the last century Osborn<sup>2</sup> had already come to the conclusion that the Darwinian idea was insufficient to give an explanation of the evolutionary process and, if acquired characters were not inherited, there was some unknown factor in evolution. He then began a search for this unknown factor along palæontological lines, and before his death, after intensive research, he claimed to have discovered it in what he called *aristogenesis*.<sup>3</sup>

The study of pre-Darwinian zoology, embryology and comparative anatomy brought to light ten "principles of bio-mechanical adaptations" which relate to the somatic origins and modifications of origins but not of species; i.e., they are concerned with ontogeny, not with phylogeny. After Darwin's time an eleventh principle, e.g., the continuity of the germ plasm, was added by Weismann. These principles are given in tabular form below (Table 5). On the other hand, the study of palæontology has revealed nine complementary principles of "adaptive bio-mechanical origin in the germ plasm". These are given in Table 6.

The application of one or all of these principles to the study and phylogeny of a group enables one to understand the biomechanical origin of the species of that group in response to the environment which shows itself as an adaptive radiation. Each of the first

<sup>1</sup> A list of Osborn's Papers on the origin of species is given in the Bibliography.

<sup>2</sup> 1891, p. 20, and 1895.

<sup>3</sup> 1934.

Table 5<sup>1</sup>*Zoologic Modification of Existing Organs, Ontogeny.*

- 1 Biomechanical onto-retrogression (Aristotle), degeneration, atrophy of organs.
- 2 Biomechanical onto-progression (Aristotle), development, hypertrophy of organs.
- 3 Biomechanical onto-compensation (Aristotle), metatrophy and eutrophy of organs.
- 4 Biomechanical onto-economy (Aristotle), metatrophy and eutrophy of organs.
- 5 Biomechanical onto-allometry (Lamarck-Darwin), allometrons, changes of proportion in organs.
- 6 Biomechanical co-adaptation (St. Hilaire), co-ordination, correlation of organs.
- 7 Biomechanical onto-acceleration (v. Baer) into earlier growth stages of organs.
- 8 Biomechanical retardation (v. Baer) into later growth stages of organs.
- 9 Biomechanical auto-adaptation (Goethe) through principles 1 to 8.
- 10 Biomechanical onto-saltation (St. Hilaire), sports, discontinuities.
- 11 Biomechanical continuity of germ plasma (Weismann).

Table 6<sup>2</sup>*Palæontologic Origin of New Characters, Phylogeny.*

- 12 Biomechanical phylo-mutation (Waagen, 1869), orthogenesis in new characters.
- 13 Biomechanical phylo-trend "mutations-richtung" (Neumayr) in new characters.
- 14 Biomechanical phylo-acceleration (Hyatt, 1880) in the evolution of single characters.
- 15 Biomechanical phylo-retardation (Hyatt, 1880) in the evolution of single characters.
- 16 Biomechanical phylo-continuity (Osborn, 1889-1931), discontinuity in single characters.
- 17 Biomechanical phylo-potentiality (Osborn, 1889-1931) in the origin of new characters.
- 18 Biomechanical phylo-predetermination (Osborn, 1889-1931) in the origin of new characters.
- 19 Biomechanical phylo-rectigradation (Osborn, 1889-1931) in the origin of single characters.
- 20 Biomechanical phylo-aristogenesis (Osborn, 1889-1931) in the rise of grouped characters.

<sup>1</sup> From Osborn, 1931 and 1932.<sup>2</sup> *ibid.*,

19 principles given in the accompanying tables refers to the method of production or origin of some new organ or character. The last one refers to the biomechanical evolution of grouped characters or series of characters. To this principle Osborn has applied the name of *aristogenesis*, or *creative evolution*. The study of these principles applied to large numbers of living and fossil animals has enabled Osborn<sup>1</sup> to define this concept as follows: "*Aristogenesis is the gradual, secular, continuous, direct, reactive, adaptive origin of new biomechanisms. It is a creative process from the geneplasm of entirely new germinal characters. It is the orderly creation of something better or more adaptive. Certain lines of descent are distinguished by the potentiality of creative origin from the geneplasm of new adaptive biomechanisms. Germinally predetermined origin of new characters tends towards betterment, arises independently, in widely separated geographical areas, at the same or different aristogenic rates. Aristogenesis is a secular genetic and adaptive reaction rather than an immediate adaptive reaction to new habit or environment as in Lamarck's theory. Aristogenes are independent in origin and an early development of the Natural Selection principle of Darwin.*"

Adaptive radiations are expressed in two chief ways by means of (a) allometrons, or (b) aristogenes. Allometrons express an independent or particulate adaptive radiation which was known in some measure before Darwin's time. Allometric change is seen in the modification of existing organs in animals. Osborn found that the study of many fossil and existing animals revealed changes in the proportionate sizes of their limb bones, heads, tusks, etc., and these changes could be expressed in units as allometrons. Comparative study of series of allometrons revealed how, for example, the various types of locomotion of horses, elephants etc., had arisen. An increase of one bone in a leg of, say, a fleet-footed horse can be correlated with a decrease in the corresponding bone of, say, a slow-moving elephant in a series of these animals, showing an increase of speed in one direction and an increase in weight in another. Analogous changes can be observed in the limbs of all quadrupeds. An example of this allometric change is given in Table 7, which shows the allometric adaptations in the horse and the elephant.

Inasmuch as allometrons are adaptive they are brought about by internal and external forces and Osborn enumerates four of these, namely, (a) physical environment, (b) living environment, (c) influences of habit, and (d) predispositions and potentialities

<sup>1</sup> 1933, p. 700.

of heredity. Generally speaking, then, allometric changes are not predetermined, and do not follow a constant trend. As they are based on proportionate measurements of bodily features, they are intimately concerned with the definition of, and changes in, species.<sup>1</sup>

On the other hand, aristogenes are adaptive characters which arise directly from the germ plasm, and initiate evolutionary trends. At first, Osborn called them rectigradations and compared them with the "*Mutationsrichtung*" of Neumayr.<sup>2</sup> He

Table 7<sup>3</sup>*Allometric Adaptations in the Horse and Elephant.*

Bone of limb	Length of bone expressed as % of total length of limb	
	Speed: horse	Weight: elephant
Femur	27.1 (shortened for speed)	48.6 (lengthened for weight)
Tibia	31.7 (constant)	34.3 (constant)
Pcs	41.1 (lengthened for speed)	17.1 (shortened for weight)

discovered these aristogenes in studies of the phylogeny of the elephants, horses and titanotheres, that is, in palæontological series of great geologic age. His best example is probably shown by his investigations of the changes in the grinding teeth of the long-jawed Mastodons of the Siwalik Hills of Northern India. The series started in Africa in the eocene period with the type called *Moeritherium Andrewsii*, and ended in India in the upper miocene period as the type *Triplophodon* after a time period of about twenty million years. During this period allometric changes took place in the third inferior grinding tooth. The teeth increased vastly in bulk, but the allometric index decreased by about a hundred per cent. The grinding tooth of *Moeritherium Andrewsii* started with 7 conical elements (or aristogenes), while *Triplophodon macrognathus*, 20 million years later, had 37 conical elements, that is, 30 new aristogenes had arisen in the period from eocene to miocene. A detailed study of the geological strata shows that the new conical elements, or new aristogenes, originate spontaneously, i.e., from the germ plasm, but in response to some new adaptational requirement. Roughly speaking,

<sup>1</sup> Adapted from Osborn, 1934, p. 200.

<sup>2</sup> 1932, p. 59.

<sup>3</sup> 1926 a and b.

Osborn found that one new aristogene arose for every million years. Some details of these changes in the whole series are given in Table 8 below.

Table 8<sup>1</sup>*Aristogenic and Allometric Origin of Mastodon Species.*

Geological Stratum	Species	No. of Aristogenic conical elements	Index No. of Allomecons
Eocene ..	Moeritherium Andrewsii ..	7	73
	Palcomastodon intermedius ..	7	63
Oligocene	Phiomia Osborni .. ..	10	54
Lower Miocene	Trilophodon Cooperi ..	20	43
	Trilophodon Cooperi ..	19	43
	Trilophodon palæindicus ..	20	42
Upper Miocene	Trilophodon chinjiensis ..	25	40
	Trilophodon macrognathus ..	37	36

Osborn builds up his idea of aristogenesis from his palæontological data. He finds that the study of long lineages of animals has led to the discovery of a large number of biomechanical principles which are logically expressed in a principle of aristogenesis leading to a new concept of evolution. Aristogenesis is not therefore vitalistic in content but it is, as Osborn remarks, "a matter of potentiality", and he finds that his idea is in some senses an echo of some of the ideas of Aristotle and of St. Augustine's "*potentialiter atque causalitas*".<sup>2</sup> The principles of palæontology and aristogenesis, which are worked out from adaptive characters, while they may tell us how evolution has occurred, do not tell us anything about the causes of the origin of species. According to Osborn, to approach this problem requires a completely new concept of evolution.<sup>3</sup> It seems possible, however, that aristogenesis may have put us on the right track, and we may conclude by giving some of the palæontological opinions made by Osborn to the 1931 London meeting of

<sup>1</sup> Adapted from Osborn, 1933, p. 701, and 1934, p. 224.

<sup>2</sup> Osborn, 1934, p. 230.

<sup>3</sup> 1932.

the British Association.<sup>1</sup> He maintains that "Palæontology is the two-edged sword of Biology: it cuts the hypotheses unfit to survive, it strengthens hypotheses fit to survive. It calls for conceptions of a new and physico-chemical order to supplant outworn hypotheses dating back to Empedocles (600 B.C.). It disestablishes the 'entelechy-vitalism' of Aristotle (300 B.C.) and establishes his 'firm and undeviating order of Nature'. It establishes the 'direct action of environment' (Buffon 1755—Wagner 1870). It disestablishes the habit-inheritance of E. Darwin and Lamarck (1790—1809) and establishes habit through onto-adaptation, as a guiding principle in evolution. It disestablishes the third and fourth principles of C. Darwin (1859) and establishes selection as a universal and outstanding principle from the beginning of time. It firmly establishes the 'W. Mutations' of Waagen (1869). It establishes 'the continuity of germ plasm' and the 'separateness of somaplasm' of Weismann (1880). It disestablishes the hyperselection of the neo-Darwinians. It excludes entirely from bio-mechanical evolution the 'D. Mutations' of de Vries. In its earliest as well as its latest phases palæontology undermines the primitive idea of *created-evolution*; of recent years it firmly establishes *creative-evolution* or 'aristogenesis'."

### 3. LOTSY'S THEORY OF EVOLUTION BY MEANS OF HYBRIDIZATION

In his *Evolution by Means of Hybridization*, Lotsy (1916) has built up a genetic theory of evolution of limited applicability to the general theory of organic evolution, but complete and logical so far as it goes. By his definition of "species" he immediately limits the range of variations covered by his theory. He defines a species as follows:<sup>2</sup> "A species consists of the total of individuals of identical constitution unable to form more than one kind of gametes." Experimentally the purity of the gametes is best determined by examining the constitution of the  $F_1$  individuals. If these are uniform, then the parents can be presumed to be pure. Even so, it is extremely difficult to be absolutely certain that any given form is homogametic, i.e., genetically pure in all characters. Thus, in Lotsy's opinion, the problem of evolution becomes not so much the problem of the origin of species, but rather the problem of the origin of *individuals* of different constitutions which together

<sup>1</sup> 1931, p. 57.

<sup>2</sup> 1916, p. 23.

form the organic life of the earth. In one sense this theory is a return to the idea of Agassiz that it is the individual which is of importance while the species is a mere abstraction with no actual existence. On the other hand, hybridization of individuals lies at the basis of modern genetical experimentation, and from this fact has arisen such ideas as Goldschmidt's conception of micro-evolution. Lotsy, however, does not deny the species actuality.

According to Lotsy the real problem of the origin of species was solved by Mendel when he showed that new forms could arise in the  $F_2$  generation by the fusion of unlike gametes produced in the  $F_1$  generation in a cross. Referring to this Lotsy<sup>1</sup> says: "By crossing two monogametic individuals of different constitution, one consequently obtains a polygametic hybrid which is the source—and up to the present *the only known source*—of the origin of new forms, some of which are heterozygotes, others of which are homozygotes, e.g., new species." By isolation of such homozygotes we can obtain as many individuals of a new species as we like. Hence Lotsy considers that new species can just as well originate from hybrids as from pure species in which a change or mutation must first of all occur. Indeed, we can rarely be certain that what is called a mutation is indeed a new change or not the product of previous distant hybridity. It follows that new species can arise monophyletically or polyphyletically and also polytopically, that is, at different places independently of each other. If heredity is "the transmission of the characters of the parents to the offspring" then, according to Lotsy, we know nothing about it in spite of the various particulate theories of heredity. These may help us to understand the distribution of gametes in hybrid populations, but they tell us nothing about heredity in homozygotes or pure breeding species.

Lotsy contends that the Linnean, or the species in the ordinary Linnean sense, is really a vestige, and consists of a relatively small number of different types left over from many types produced by a previous crossing. In nature selection evidently prunes down the results of natural crosses and gives us what we call a Linnean species. Within the Linnean species themselves crossing is free, but some Linneons are sterile or are prevented from crossing with others owing to aversion, isolation, or some other natural cause. Thus it is nature herself which separates the Linneons; they are

<sup>1</sup> 1916, p. 53.



not merely artificial groupings invented by naturalists for convenience. According to Lotsy, when obstacles to the crossing of Linneons are removed, what is called progressive evolution begins, leading to the production of new species. Crossings between groups, or Jordanons, within the Linneon, leads to what is called degressive evolution, or the production of new varieties.

Variations among domesticated animals and plants, instead of showing that organisms have an inherent capacity to vary, as Darwin thought, merely point out the effects of selection and isolation of individuals, which have arisen from heterozygotes. There is plenty of evidence that new individuals have arisen by crossing of Linneons in nature and in experiment. Lotsy cites the new forms of *Antirrhinum* produced by hybridization.

Lotsy's theory is also supported by the general geological history of species. Geology teaches us (a) that classes of organisms originated in remote times, (b) that when a new class appears it does so with many different forms, and (c) that as time passes the number of these forms diminishes and they become "reduced". For example, we have but to compare the abundance of the mesozoic cycadophytes, the coal measure Lycopodiales or Equisetales, with the present members of these classes. Lotsy points out that the present day scarcity of these classes agrees with the results which we would expect after the crossings of various Linneons. At the beginning many different forms would appear in the progeny, but in the course of time the number of these would decrease because of selection, isolation, sterility, etc., until only a few forms remained to make up the Linneon. As he<sup>1</sup> says: "*Crossing therefore is the cause of the origin of new types, heredity perpetuates them, selection is the cause—not of their origin as was formerly supposed—but of their extinction.*" Selection eliminates types and individuals and thus prevents crossing, or reduces its incidence, and hence limits the production of new individuals and species. At the present time we live in a period when many classes are all but exterminated, and in which no new classes have yet been formed. In the absence of experience, therefore, we cannot *know* how new classes arise, but we can infer that they may arise through hybridization.<sup>2</sup>

<sup>1</sup> 1916, p. 28.

<sup>2</sup> There is a good deal of evidence based on recent researches indicating that in all probability many of the wild roses, brambles, hawkweeds and dandelions, which now reproduce largely apomictically, are of hybrid origin.

## 4. WILLIS' THEORY OF EVOLUTION BY DIVERGENT MUTATION

(a) *The Age and Area Theory*

Willis has developed his Age and Area Theory over a period of years in many papers and books.<sup>1</sup> The later theory of evolution is directly dependent upon this hypothesis.

Studies of the distribution of the flora and fauna of the world have shown that some species are confined to only one country. These are spoken of as *endemic species*. Willis found that species endemic to an island or other region were often also endemic or confined to a localised area of that island or region but showed no peculiar adaptation to it. He then began a detailed study of the flora of Ceylon, Peninsular India, and, later, of New Zealand. A critical examination of Trimen's *Flora of Ceylon* showed:—(a) that of the 809 species of flowering plants endemic to Ceylon, less than 200 are confined to single spots, and (b) that the endemics are found on areas of various sizes in which the number of endemics grows smaller as one goes up the scale from the smallest to the largest areas. This means that there is a large number of endemics occupying small areas, and a small number occupying large areas.

In Trimen's *Flora* the species are marked as being very common (VC), common (C), rather common (RC), rather rare (RR), rare (R) or very rare (VR). Willis found that, generally speaking, a VR species occurred in one place only (or perhaps two places close together), while the R and RR species covered areas that overlapped in every possible way. In no place did the areas occupied by two endemic species coincide. Many endemics were found on mountain tops. Obviously an endemic species may either have been evolved within the area it at present occupies, or have occupied a much larger area from which it has gradually been ousted until it is left in its present single area; in other words, it may be in the process of dying out, a relic. According to the theory of natural selection, new species are evolved by means of local adaptations. Willis, however, points out that if the two species A and B grow in overlapping areas both must be growing in the coincident portion. What is it then that prevents A from growing into B's territory and B into A's? As Willis<sup>2</sup> remarks: "But when one considers that the conditions are never the same from one spot to the next, nor from one year to

<sup>1</sup> A selection of his writings is given in the Bibliography. His views on the Age and Area Theory are fully stated in his book, *Age and Area*, 1922.

<sup>2</sup> 1922, p. 57.

the next, this would mean a most wonderful adaptation if the species were not to grow into each other's territory, especially when one remembers the many more widely distributed species that occur in both." According to Willis, Darwinian ideas of local adaptations are, then, untenable. Again, the contention that endemics are relics which represent dying out species is considered by Willis to be improbable as there are more VR species than RR or R. If endemics were relics, it would also be difficult to explain the increasing graduation in the numbers of endemics as we pass from large to small areas.

Later Willis divided the flora of Ceylon into three groups: (a) those endemic to Ceylon, (b) those found in Ceylon and Peninsular India, and (c) the "wides", or those with a still wider distribution. On then enumerating the various species he found that the endemics of Ceylon were "VC 19, C 90, RC 139, RR 136, R 192, VR 233, increasing fairly steadily from top to bottom of the list." On the other hand, the "wides" occurred in the reverse order namely: VC 221, C 462, RC 313, RR 209, R 159 and VR 144.<sup>1</sup> Further statistical investigations showed that the most widely distributed species in Ceylon were, on the average, the "wides", or those also showing the greatest distribution beyond Ceylon and Peninsular India; next followed those reaching to Peninsular India; the least widely distributed species in Ceylon were those confined to this island.

The key to these problems of plant distribution was seen by Willis to be age. He realised that in itself age effects nothing, but maintained that the passage of time allows for the operation of the various factors affecting distribution, and he suggested an explanation of the distribution of the species of Ceylon.<sup>2</sup> He supposed the "wides" to be (on the average) the oldest, and to have been the first arrivals in Ceylon. He thus allowed them sufficient time to spread to the largest extent and suggested that, on the way, they might give rise, perhaps somewhere south of the middle of the peninsula, to the species not found in Ceylon and Peninsular India; these would be the next oldest and would spread in Ceylon to the second degree of distribution. The Ceylon endemics would arise in Ceylon, and on the whole probably later still, from one, or more likely both, of these groups, and, being the youngest, they would have spread the least.

<sup>1</sup> 1922, p. 59.

<sup>2</sup> 1922, p. 61.

Confirmatory evidence for this view was obtained from the floras of New Zealand, Australia, Jamaica and the Hawaiian Islands.<sup>1</sup> It was clear to Willis from these studies that age is related to the area occupied and he then<sup>2</sup> formulated his theory. Willis writes: "The area occupied at any given time, in any given country, by any group of allied species at least ten in number, depends chiefly, so long as conditions remain reasonably constant, upon the ages of the species of that group in that country, but may be enormously modified by the presence of barriers such as seas, rivers, mountains, changes of climate from one region to the next, or other ecological boundaries, and the like, also by the action of man, and by other causes."

(b) *Evolution by Differentiation or Divergent Mutation*

Further extended studies, and indeed the age and area theory itself, brought Willis to the fore as a strong critic of the currently held Darwinian natural selection theory. His later mature conclusions are given in detail in his book *The Course of Evolution*<sup>3</sup> which is probably the best modern detailed criticism of the theory of natural selection.

The author endeavours to show that nature presents many cases of so-called adaptation which are inexplicable upon a selection basis but the existence of which, when interpreted in terms of Age and Area, becomes quite clear and straightforward. Willis' studies on that peculiar family of water plant the *Podostemaceae* led him to the conclusion that the large amount of variation shown by forty genera and 160 species of this family had nothing whatever to do with their adaptation to mountain torrents. He writes<sup>4</sup> : "It would almost seem as if, in cases like this, if not perhaps in most, *evolution must go on whether there be any adaptational reason for it or not.*" Throughout the family *Podostemaceae*, in spite of the unique uniformity of the growing conditions, an "inescapable force urging dorsiventrality" was plainly evident. The only explanation of the production of the various species, and taking this force or urge into account, was, it seemed to Willis, to account for their origin by means of mutations, or sudden jumps.

<sup>1</sup> Willis, 1921.

<sup>2</sup> 1919, p. 479, and 1922, p. 63.

<sup>3</sup> 1940.

<sup>4</sup> 1940, p. 21.

The key to the evolutionary problems which Willis created for himself by his distributional studies was found when he came to the conclusion that selectionists attacked the problems from the wrong end. According to a selectionist a variety, if successful, is an incipient species. The Darwinian evolutionist consequently works *backwards* from the variety to the sub-species, species, genus, family and so on. Willis<sup>1</sup> quotes H. B. Guppy (1917) as being the first person to point out that the Darwinian attempts to work out evolution backwards. Guppy contends that, as nature always works from the simple to the complex, from the general to the particular, then the true path of evolution leads from the family to the genus, species, variety, etc.

From the work done on the age and area idea a general rule emerged which was shown by what Willis calls "the hollow curve of distribution". This curve suggests statistically that the distribution of plants is chiefly due to accidental causes, and is not determined by adaptation, as demanded by the selection theory. The flora of Ceylon provides an example of the hollow curve. Willis<sup>2</sup> writes that the Ceylon flora consists "of  $573/1$  (573 genera each with one species in Ceylon),  $176/2$ ,  $85/3$ ,  $49/4$ ,  $36/5$ ,  $20/6$ , and so on. If one takes the first few numbers, one finds that the numbers to right and left of any single number (e.g., of  $176/2$ ) add up to more than twice as many ( $573/1 + 85/3 = 658$ ) as itself." If these figures are graphed then it is seen that the resultant curve is hollow, i.e., the reverse of the ordinary type of curve. Willis obtained many hollow curves from examinations of other flora and also from the statistical grouping of areas covered by species in a genus, or genera in a family, with respect to the number of species. Logarithmic curves made from these hollow curves are practically straight lines. According to Willis, it follows that there is a definite law governing distribution of plants and their evolution.

The fact that the statistical grouping of species, genera, etc., in the manner done by Willis produces a hollow curve can be explained if we assume evolution does actually occur but that adaptation has little or nothing to do with it. The distribution of plants, then, is accidental or haphazard and investigation shows that distribution is in fact haphazard. Yule<sup>3</sup> analysed Willis' hollow curves mathematically and came to the conclusion that at "the end of certain

<sup>1</sup> 1940, p. 175.

<sup>2</sup> 1940, p. 33.

<sup>3</sup> 1924, p. 21.

intervals, probably very variable in length, a genus became two, and both as a rule survived."<sup>1</sup> If this happened, the new genus may have arisen by mutation which produced a change that was *qualitatively* different. That is, evolution is due to a process of *differentiation*.

Evolution by differentiation was first brought forward by Geoffrey St. Hilaire (1837); later Owen and Mivart recognised the principle involved in this idea. Then Guppy, and at about the same time, Willis, began to examine it in detail. The essential feature of evolution by differentiation is that it proceeds from the family to the species and variety. According to Guppy<sup>2</sup>, in early times, when the climate was damp, families were formed by means of large mutations which increased in number and variety by further large mutations as time went on. Later, as the climate began to differentiate and become drier, the speed of mutation increased but the size of the mutations decreased, producing genera, species, etc. Because the originals survived as well as the descendants families and genera became larger, producing the hollow curve of distribution.

Willis gives much evidence to support this idea of evolution by differentiation, but he prefers to call it evolution by means of divergent mutations. He applies to the theory several practical tests of a numerical, morphological, taxonomic and distributional nature which show that the theory allows for many features possessed by organisms which are difficult to account for by means of the natural selection of small variations. The theory of Willis depends on the production of mutations both large and small and, whereas few mutations have actually been found in nature, the assumption of their occurrence enables us to build up a theory of evolution which accords equally well with the morphology and distribution of organisms and also stands the test of prediction. As it overcomes all the difficulties of the natural selection theory it does not make a fetish of adaptation. As Willis<sup>3</sup> states: "Natural selection is no longer to be regarded as the mechanism of evolution; it does not choose what shall be involved (i.e., in evolution), but it decides in each case, individually, what should be allowed to live. Probably, the bulk of the structural characters make little or no difference one way or the other, and so are indifferent to natural selection. Evolu-

<sup>1</sup> See Willis, 1940, p. 173.

<sup>2</sup> 1906.

<sup>3</sup> 1940, p. 175.

tion ceases to be a mere matter of chance, and comes into that scheme of things of which Jeans has said that all the pictures which science draws of it are mathematical pictures." What causes evolution to go on is as yet unknown.

#### 5. GOLDSCHMIDT'S IDEAS OF MICRO- AND MACRO-EVOLUTION

In an outstanding study of the processes of evolution Richard Goldschmidt<sup>1</sup> has analysed thoroughly the relation between mutations and evolution. He brings together a mass of fact and evidence to support his thesis, and his conclusions may be said to represent the most advanced synthesis of causal evolutionary theories so far published. Goldschmidt's ideas may mark the beginning of a new phase in which the importance of the gene as the mechanical basis of heredity is giving way to another conception involving the whole chromosome as the real basis of change.<sup>2</sup>

It is becoming increasingly recognised that the processes of evolution depend, not on one, or a few, causal factors, but on *all* the possible factors or influences within or without the organisms which are evolving. What, on the Darwinian conception of evolution by means of natural selection, is seen as due to chance is inferred from this presentation of the newer view of Goldschmidt as merely a stage in a dynamic process which has unity in the form of a single reaction system in each species as its first law—a unity which is attained by the operation of a simple, efficient, but unfailling mechanism. Evolution is then seen to proceed through an ordered series of events in the natural organic world. Thus, while Goldschmidt does not anywhere say this, he nevertheless succeeds in fulfilling the requirements of the deeds of the Silliman Lectureship on which his book was founded, by demonstrating the operation of law and order in the natural world.

Goldschmidt recognises two distinct kinds of evolution which he calls *micro* and *macroevolution*. By the former he means evolution within the species, and by the latter he means the evolution of species and all higher categories. He sets out to show that the course and causes of the process of microevolution differ considerably from those of the process in macroevolution. While, as we have seen, gene or point mutations have been recognised

<sup>1</sup> 1944.

<sup>2</sup> And see Chapter 8, Sect. 5, for a discussion of the gene as a unit, and its influence in evolution and heredity.

for some time now in spite of the fact that so many of them are non-viable or deleterious to the organism possessing them, they are still regarded as the raw material on which evolution works. Many of these gene mutations are inherited in a simple Mendelian way. Not all mutations are non-viable, however, and undoubtedly some adaptations which can only have arisen by mutation have been described from nature. For example, the melanic forms of *Lymantria monacha* L., where a series of wild mutants varying in colour from white to black was found, may be cited.<sup>1</sup> The mutants were due to the individual and combined action of three dominant mutant genes, one of which was sex-linked. Another example is furnished by Heslop Harrison's cases of industrial melanism in *Selenia bilunaria*, or in local races of *Oporabia autumnata*.<sup>2</sup> Goldschmidt considers that these and many similar cases are examples of natural changes in organisms which are furthermore adapted to their habitat.

It is becoming increasingly recognised, however, that these, for the most part deleterious, gene mutations are only the more or less obvious changes which the investigator works with because they are easily detected as changes in the species. Goldschmidt and others contend that, over and above these obvious changes in organisms, nature is continually producing very slight differences whose phenotypic effects are very small. These are the so-called micromutations and, if adaptive, they may enable the species to survive in a multitude of habitats.

In writings on ecology different taxonomists have used the word "species" in so many different senses that a state of chaos prevailed; each systematist followed his own fancy and, in extreme cases, anything supposedly new was designated a new species. However, with the further study of geographical distribution, it has become evident that in many cases similar forms of organisms comprise a natural unit called a *rassenkreis* extending over a definite geographical range. Within the limits of the *rassenkreis* many geographical races could exist, each race adapted to some specific environment. The geographical races themselves within the *rassenkreis* may be phenotypically distinct enough or they may grade one into the other through minute differences due to the occurrence of micromutations. Those races situated near to each other resemble their neighbours, but races at the limits of the

<sup>1</sup> Goldschmidt, 1944, p. 15, and 1920.

<sup>2</sup> 1920.



geographical range may vary considerably from each other, i.e., there may be more and larger differences between these than between those living nearer to each other. All of them are inter-fertile. Geographical race is a term usually applied to animals, the corresponding term in plant-ecology is that of the ecotype. A more general term, the cline, has recently been introduced by J. S. Huxley,<sup>1</sup> which by the use of various prefixes can be used to cover all environmental conditions and situations.

The differences between races, or forms, of these types, so far as they have been investigated, are shown to be heritable but do not generally follow any simple Mendelian system. They seem to be due to the operation of multiple allelomorphs. Each allelomorph in a long series represents a micromutation, and the differently combined accumulations of them in the organisms are considered to produce the slight mutations and apparently continuous phenotypic variations. Hence evolution within the species between the various geographic races, clines and lower categories takes place through the piling-up of micromutations. This process is called microevolution. Goldschmidt<sup>2</sup> writes:—"The genetic picture, within the species, then, agrees with Darwin's ideas, formulated in the recent genetic era, as the occurrence and accumulation of micromutations, though occasionally also a larger mutational deviation may be added to the process of diversification." Goldschmidt considers that microevolution is the process by which a true species, or *rassenkreis* of sub-species, adapts itself to the varying conditions of the habitat in which it lives.<sup>3</sup>

Next, Goldschmidt considered the limits of microevolution. It seems to have been generally accepted by taxonomists, and also by geneticists, that the good sub-species, or the geographic races, at the extreme range of the *rassenkreis*, were, in Darwin's phraseology "incipient species"; this means that such a sub-species, given a chance, such as isolation from the original type, would develop further on its own and become itself a good species. Such a view fits in with the true Darwinian idea, but it takes for granted the assumption that change would continue to occur in the same direction in the isolated sub-species almost indefinitely until something radically new emerged. The mathematical selectionists (Fisher, Wright, Haldane, etc.) have accepted this assumption and on it have

<sup>1</sup> See Huxley, J. S., 1939; 1940, p. 31 *et seq.*, and 1942, Chap. 5.

<sup>2</sup> 1944, p. 101.

<sup>3</sup> 1944, p. 107.

built up an elaborate mathematical treatment of selection and evolution of mutants within populations in support of the ordinary Darwinian conceptions. But Goldschmidt contends, and brings evidence to show, that micro-evolution, or change due to the accumulation of micromutations, is limited in its extent, and the deviations or micromutations lead to blind alleys and dead ends. For example, once a colour mutant attains true blackness it cannot change any further in that direction. Goldschmidt<sup>1</sup> sums up this view by stating: "The contents of this chapter, as well as all the data presented thus far and to be presented below, show that the neo-Darwinian conception which works perfectly within the limits of the species, encounters difficulties and is not sustained by the actual facts when the step from species to species has to be explained. Selection will certainly be involved also in the accomplishment of this decisive step, but we shall see that selection in nature probably has much easier work than that required by the neo-Darwinian idea of slow accumulation of micromutations." And again:<sup>2</sup> "*Sub-species are actually, therefore, neither incipient species nor models for the origin of species. They are more or less diversified blind alleys within the species. The decisive step in evolution, the first step towards macroevolution, the step from one species to another, requires another evolutionary method than that of sheer accumulation of micromutations.*"

Goldschmidt then proceeds to consider the phenomena of macroevolution by which is meant the evolution of species from species and of higher groups up to the phylum.

In brief, he notes that, when geographic variation of species is studied along with the geological history of the species it is found that the geographic races have all been formed after isolation in the more recent Tertiary and Glacial Ages. He remarks that this seems to show that differentiation within the species is a very slow process indeed, and one which enables it to spread into new areas. On this basis, if evolution of higher categories proceeds in the same way as differentiation of forms within the species, i.e., by the slow accumulation of minute differences, then an absurdly long stretch of time would be necessary to account for the process.<sup>3</sup> Further, species studies, or studies within a *rassenkreis* of forms, show that between such true species there are gaps unbridgeable by micromutations. This seems to indicate

<sup>1</sup> 1944, pp. 138-139.

<sup>2</sup> 1944, p. 183.

<sup>3</sup> See Goldschmidt, 1944, p. 168.

that the order of change within the species range is in a different category from the order of change external to the species range.

In chapters 7 and 8 we discussed the various types of changes which affected the nuclei of cells, leading to phenotypic variations. It was pointed out that, according to the ordinary neo-Darwinian view, large mutations produced by gross chromosomal alterations, such as polysomy, and internal changes, such as translocations, inversions, duplications, etc., are of little value in the evolutionary processes. This view is based on the assumption that changes of these kinds either merely lead to upset of the balance of the chromosomes within the reproductive parts, i.e., they upset the gene complex, and so are not stable, or merely cause re-arrangements of the genes already present and so lead to the production of nothing which is intrinsically new. Granted the truth of the gene theory, this assumption is perfectly logical, and, indeed, it must be made if evolution is to be interpreted in terms of Darwin's ideas. According to the same ideas, the only known method of producing anything new is by means of gene or point mutations, when one gene changes into something completely new. There is then a chance for evolution to occur if this new gene becomes incorporated into the species.

Goldschmidt, however, reverses this idea and holds that, even on the basis of the gene theory, evolution through the agency of the selection of gene mutations, or evolution by means of micro-mutations, can occur only within the limits of the species, where it obviously furnishes a mechanism which enables the species to adapt itself to local environmental conditions. He considers that for the evolution of species and higher categories gene mutations are of no use, chromosome patterns must be altered. These alterations would involve complete re-arrangements of the chromosomal material, resulting in new chemical reaction systems which, by their very nature, would have a large effect on development, etc. This process would result in the appearance of some large phenotypic variation, that is, in the appearance of something new separated from the original form by a "bridgeless gap". Goldschmidt calls this process *macroevolution*. To accept the idea of macroevolution means a return to the fundamental idea behind the original theory of heterogenesis.

The chromosome is a unit, and behaves as such. But in current views it is thought to contain genes arranged in order along its length. A gene acts in conjunction with the genes in its neighbourhood,

which means that it is a part of a system. Inasmuch as the chromosome is material, this system may be regarded as a chemical system. In Goldschmidt's opinion a single chromosome furnishes a single reaction system due to a definite intrachromosomal pattern. Before species formation can occur a new pattern producing a new reaction system must be established. This means that the chemical composition of the chromosome must undergo a major change; a mere alteration of the side chain of a large molecule of protein would probably not modify the reaction system sufficiently. According to Goldschmidt, the genetic effect of a drastic alteration of chromosomal pattern would be sufficient to account for macroevolution. He suggests the term *systemic mutation* to describe the change of pattern which produces such a large effect.

The varying morphology of the individual chromosomes sometimes enables us to separate species or higher units, but in many groups the morphology of the chromosome complements is identical. Hence the production of a new species may or may not involve a change of chromosome morphology. There are, however, several known examples in which genetic or geographic races are only distinguishable by chromosome analysis. For instance, Goldschmidt<sup>1</sup> gives the example of the three geographic races of *Gryllotalpa grylloides* (the mole cricket) which differ only in chromosome numbers (these are 12, 15 and 14-17), and in the sex chromosomes which were studied by de Winiwarter<sup>2</sup>, who found that they differ in morphology according to the locality of the race. The inversions in races of *Drosophila azteca* and *D. pseudo-obscura* have already been mentioned.<sup>3</sup>

So far studies of this kind have been carried out only in *Diptera*. In this group the salivary gland chromosomes present favourable material for detailed examination.<sup>4</sup> The presence of inversions has been inferred in many organisms from the occurrence of chromosome bridges during the meiotic divisions. In fact, Goldschmidt considers that inversions and similar chromosomal changes provide the mechanism by which macroevolutionary processes are brought about. Genes, as such, play no part in these processes. It is the reaction system of the chromosome which counts.

Further indirect evidence which Goldschmidt brings forward in

<sup>1</sup> 1944, p. 187.

<sup>2</sup> 1937.

<sup>3</sup> See page 234.

<sup>4</sup> See Sturtevant and Dobzhansky, 1936; Dobzhansky and Sturtevant, 1938; Dobzhansky and Socolov, 1939; and Dubinin, Socolov and Tiniakov, 1937.

support of his idea that the pattern of the chromosome is the all-important directive of the evolutionary status of the organism is the occurrence of chromosomal changes such as translocations, deficiencies and duplications, which produce phenotypic effects corresponding to mutations. In genetic theory these conditions produce what is called a *position effect* in reference to the altered position of the genes of the chromosome concerned. The essential point is that position effect alters the pattern of the chromosome and consequently its reaction. The magnitude of the position effect is sometimes so small as to be indistinguishable from a point mutation, leading some geneticists to think that gene mutations are in fact just very small changes of position of chromosomal material. If this is so, the idea of the gene is rendered unnecessary in theories of evolutionary causation.

Goldschmidt's views are so important that we would like to sum up the account of them above by quoting a suitable paragraph. He supports all of his statements with abundant examples which we cannot even mention here. He says:<sup>1</sup> "Systemic mutation (or a series of such), then, consists of a change of interchromosomal pattern. This is what is actually found taxonomically (the bridgeless gap) and cytologically. Whatever genes or gene mutations might be, they do not enter this picture at all. Only the arrangement of the serial chemical constituents of the chromosomes into a new, spatially different order, i.e., a new chromosomal pattern, is involved. This new pattern seems to emerge slowly in a series of consecutive steps, as the work just reported indicates. These steps may be without any visible effect until the re-patterning of the chromosome (re-patterning without any change of the material constituents) leads to a new stable pattern, that is, a new chemical system. This may attain a threshold of action beyond which the physiological reaction system of development, controlled by the new genetic pattern, is so basically changed that a new phenotype emerges, the new species, separated from the old one by a bridgeless gap and an incompatible intrachromosomal pattern. 'Emergent evolution' but without mysticism! I emphasize again that this viewpoint, cogent as it is and, in my opinion, necessary to an understanding of evolution, is to be understood only after the fetters of the atomistic gene theory have been thrown off, a step which is unavoidable but which requires a certain elasticity of mind."

<sup>1</sup> 1944, p. 206.

As Goldschmidt implies, to drop the idea of the gene from evolutionary genetic speculations will require a great mental effort on the part of geneticists and evolutionists who have spent so many years in trying to reconcile Darwinian ideas, the mutation theory and the gene theory into a synthesis of one grand causal theory of evolution. It is to be expected, therefore, that Goldschmidt's views will meet with criticism. We need only mention the views of one writer about them. Dobzhansky, undoubtedly one of the greatest geneticists, rejects Goldschmidt's views several times in his book *Genetics and the Origin of Species* chiefly on the grounds that systemic mutations have not yet been seen and that evidence can be brought to disprove his views. For example, Dobzhansky<sup>1</sup> points out that Goldschmidt's theory "virtually rejects evolution as this term is usually understood (to evolve means to unfold or to develop gradually)."

Etymologically this may be the meaning of the word, but, as this account of evolution has shown abundantly, historically the word connotes change, a change from one species into another, whether sudden or gradual. The French use the word *Transformisme* for our English word and this French word more accurately expresses what all natural historians mean by the process. There is in fact a case for dropping the word evolution altogether, for obviously in English-speaking countries it savours too much of Darwinian implications.

Dobzhansky states that Goldschmidt's systemic mutations have never been found in nature, and also that pattern effects have not been shown in the majority of mutants. He also criticises Goldschmidt's views about position effects and genes as entities by appealing to the gene theory. Other criticisms concern the invariability of systemic mutations and the so-called bridgeless gaps.<sup>2</sup>

<sup>1</sup> 1941, p. 53.

<sup>2</sup> See Dobzhansky, 1941, pp. 22, 52-53, 79-80, 82, 109-110, 231, 369-370, and Huxley, J. S., 1941.

## CHAPTER 10

### THE MODERN PERIOD CONCLUDED :

#### (D) MODERN NEO-DARWINISM : MUTATIONS AND SELECTION

##### 1. THE INDUCTION OF MUTATIONS

THE mutation theory received a great impetus when Morgan and his school began their work on the genetics of *Drosophila* which resulted in the formulation of the theory of the gene which is itself one of the foundation stones of modern genetical theory. This type of heredity can only be investigated by making use of differences, i.e., of pre-existing mutations of all kinds, as the working material. Today, however, the nature of the gene is being investigated, and its very existence doubted, so that the whole concept of gene mutation in relation to evolution may soon have to be considerably modified.

It is plain that mutations to be of any value in evolution must originate from the nucleus, or at least the cell, for it is the nucleus which is chiefly concerned in heredity. The general effect of X-rays upon living cells is to disrupt the nucleus and scatter the chromosomes, causing death or producing various kinds of chromosomal aberrations such as translocations, polysomics and the like. We have already dealt with these kinds of changes: what we wish to give an account of in this section is chiefly the induction of the smaller mutations which are probably due to gene changes, or to stimuli which increase the natural rate of gene changes.<sup>1</sup>

Timofeeff-Ressovsky has pointed out several requirements in experimental work on mutations which he considers are essential before the work can be applied to the problems of evolutionary theory. These requirements are (a) the material used must be genetically pure, (b) the numbers of experimental individuals used must be large enough to give statistically analysable results,

<sup>1</sup> There is a large literature on this subject, but very good reviews are given by Timofeeff-Ressovsky (1934b) and Duggar (1936). Advantage has been taken of these reviews in the above accounts.

(c) the number of control individuals must also be large, (d) any variation produced must be analysed in order to determine its type, and (e) the manner in which the stimulus acts on the organism should be known. These requirements represent the ideal, attainable perhaps only in the more refined X-ray experiments on a few suitable organisms such as *Drosophila*. Timofeeff-Ressovsky, however, is rather dogmatic in saying that experiments which do not fulfil all of these requirements are unscientific.<sup>1</sup>

Most of the work on induced mutations has been concerned with the subjection of the organism under consideration to the effects, or influence, of some possible environmental stimulus, that is, of some agent external to the organism. This does not mean that biologists do not realise that the internal environment, or the physiological conditions within the organism, may be of some importance to the mutational process, but only that experimental work using some external factor is easier to perform, for the factor may be the better controlled.

Some studies of the relation of physiological conditions of the organism to the mutation process have, however, been carried out. For example, Hanson and Heys<sup>2</sup> showed that the rate of germ cell formation may have an influence on the rate of mutation in the germ cells. Virgin female *Drosophilas* lay a smaller number of eggs than mated females, which means that the rate of germ cell formation in the virgin flies is less than that in the mated ones. Accordingly, they irradiated virgin and mated flies with X-rays and found that the mutation rate is significantly lower in the former. In maize the gene  $A^1$  and several allelomorphs  $a^1$ ,  $a^2$ ,—etc., cause variation in the colouring of the fruit. Rhoades<sup>3</sup> found that the gene *Dt* (dotted) and its allele *dt* were situated on different chromosomes from those carrying  $A^1$  and its alleles. But the presence of *Dt* in maize along with  $a^1$  brought about an increase in the rate of mutation of  $A^1$ . Again, Sitko<sup>4</sup> produced some evidence showing that genes lying near to breaking points of chromosomes mutated rather more frequently than those situated farther away from those points. Hanson<sup>5</sup> showed that neither starvation nor anaesthesia had any effect on the rate of mutations produced by X-rays in *Drosophila melanogaster*. He noticed also that

<sup>1</sup> 1934, p. 412.

<sup>2</sup> 1934.

<sup>3</sup> 1936, 1938.

<sup>4</sup> 1938.

<sup>5</sup> 1935.



the mutation rate was twice as high in the sperm as in the egg cells. Finally, several workers have recently noticed that there is often an increased frequency of mutations in hybrids compared with the frequencies in either of the parents. For instance, Belgovsky<sup>1</sup> discovered an increased rate of mutation in the hybrid between *Drosophila simulans* and *D. melanogaster*. Sturtevant<sup>2</sup> also found an increased mutation rate in hybrids of races *A* and *B* of *Drosophila pseudo-obscura*. Harland<sup>3</sup> showed that hybridization on cotton increased the rate of mutation in some genes.<sup>4</sup>

(a) *Mutations Induced by Chemical Means*

Dobzhansky<sup>5</sup> points out that chemical agents do influence the mutation process for "It is difficult to conceive of other than chemical mechanisms for the modification of the mutability of genes. . . ." Nevertheless, practically all early attempts to induce mutations by means of chemical agents failed. Morgan, Bridges and Sturtevant<sup>6</sup> state that the following chemicals, namely, sugars, acids, alkalies, ether, arsenic, methyl alcohol, ethyl alcohol, quinine, strychnine, copper sulphate, methylene blue, lithium carbonate and lead acetate, have been used by various workers on *Drosophila* without obtaining mutations. Stadler<sup>7</sup> steeped seeds of barley in solutions of lead, barium and uranium nitrates, but the resultant plants did not produce any mutations. In experiments of this kind, especially those performed on animals such as *Drosophila*, an experimental difficulty is encountered for one can never be certain that the chemical used in the experiment penetrates the body wall and reaches the germ cells. The chemical may, however, be absorbed by the body, which it affects in such a way as to produce a corresponding effect on the germ cells. Zamenhof and Demerec<sup>8</sup> overcame this difficulty by using a substance which is known to penetrate right into the tissues. They introduced heavy water, or deuterium oxide, into the eggs and

<sup>1</sup> 1937.

<sup>2</sup> 1939.

<sup>3</sup> 1936.

<sup>4</sup> Earlier workers, such as Duncan (1915) failed either to produce mutations through various crossings, or to obtain an increased mutation rate on hybridization.

<sup>5</sup> 1941, p. 45.

<sup>6</sup> 1925, pp. 26-27.

<sup>7</sup> 1928.

<sup>8</sup> 1943.

larvæ of *Drosophila melanogaster* and found complete penetration, so much so that the water was probably used up by the tissues or cells in place of ordinary absorbed water, but no mutations resulted. Concentrations of heavy water above 60% were found to be lethal.

More recently techniques have been developed for applying colchicine drugs of the sulphonamide group to various plants, resulting in the production of polyploids. Bauer and Stubbe,<sup>1</sup> however, claim to have produced mutations in *Antirrhinum* by treating the seeds and seedlings with chloral hydrate, chloroform and other chemicals. Renewed attempts have recently been made by Russian workers to induce mutations in *Drosophila* by chemical means. Refined genetical methods were used for their detection. Some suggestive results have been obtained. For instance, several workers obtained mutations by treating *Drosophila* with solutions of iodine in potassium iodide, with copper sulphate, and possibly also with ammonia, potassium permanganate and other reagents.<sup>2</sup>

The first successful attempt to produce mutations by chemical or any other means under controlled and analysable conditions was made by Heslop Harrison and Garrett in 1926. Heslop Harrison's experiments on induced melanism in insects, although not as spectacular as those of Muller, to be described below, represent a significant sign-post along our pathway of the history of the idea of evolution, and hence a short account of his work in this direction is given. Heslop Harrison began his work on melanism in *Lepidoptera* about 1916 and it at least indicated that melanism in certain moths in industrial districts was inherited in a Mendelian way, and might be induced by suitable treatment. Heslop Harrison ascribed the prevalence of melanic forms of moths in industrial areas to the presence of metallic salts deposited from the atmosphere near collieries, ironworks, etc., on to the food plants of the insects. He remarks: "The presence of metallic salts, contaminating the food-plants in manufacturing and urban areas, might not only in itself affect the germ plasm so as to produce heritable melanism, but, in addition, might stimulate it when once induced to its maximum expression."<sup>3</sup> The association of melanism in *Lepidoptera* with industrial localities is very striking and certainly requires an explanation. Further, the induction of melanism itself is of great

<sup>1</sup> See Stubbe, 1938, 1940.

<sup>2</sup> See Dobzhansky, 1941, p. 46, for lists.

<sup>3</sup> 1920.

importance, for it is one of the few natural evolutionary changes which have recently occurred.

In his main experiments Heslop Harrison<sup>1</sup> used the early thorn moth (*Selenia bilunaria*) and the engrailed moth (*Tephrosia bistortata*). Few melanic forms of the former moth have been taken wild; it is therefore extremely unlikely that the original forms used in Heslop Harrison's work were heterozygous for melanism in all cases. With *Selenia bilunaria* he started with eggs obtained from a wild female from Sussex. When these developed, pairings were made among them and two batches of the resultant eggs were chosen. The first batch was divided into two lots. Of these, one lot served as a control and showed no melanics after three generations; the other lot were reared on hawthorn branches dipped into a weak solution of lead nitrate, and in this lot melanics appeared spontaneously in a ratio utterly unlike any suggesting the operation of a Mendelian mechanism. Having once appeared, however, the melanism was thereafter inherited as a Mendelian recessive. The other batch of *Selenia* was also halved into two lots. Of these, the first batch acted as the control, and they failed to produce progeny; the second lot were fed on hawthorn impregnated with manganese sulphate and melanics appeared which afterwards behaved as Mendelian recessives.

In the experiments on *Tephrosia bistortata* two related strains were used. One batch of eggs from Kent was divided into two lots; one of these served as the control, which after ten generations of feeding on knot grass showed no melanics; the other lot was fed on roadside hawthorn which was known to contain lead and manganese salts, and one melanic appeared in the fifth generation. It was later seen to be inherited as a Mendelian recessive. The other strain consisted of some pupæ from Hampshire. One moth emerging from these pupæ was outcrossed with a male; the resultant larvæ fed on hawthorn were all normal forms. From these a single pair were mated, and one melanic appeared in the offspring which behaved as a Mendelian recessive.

Heslop Harrison tried various kinds of matings with these insects in an endeavour to find out whether melanism behaved as a Mendelian recessive and whether the original moths could be regarded as heterozygotes carrying a hidden gene for recessive melanism. He wrote<sup>2</sup>: "It is incredible that we, who devised

<sup>1</sup> See Harrison and Garrett, 1926, Harrison, 1926, 1928.

<sup>2</sup> 1926, p. 262.

experiments with a certain end in view, should, on four separate occasions, with two distinct species brought from different districts, by the workings of chance, be the only individuals to come into possession of strains carrying latent melanism. This point in itself, in our opinion, affords a perfect answer to any attempts to explain away our results by the 'latent recessive' method." The results as they stand certainly seem to show that Heslop Harrison induced inherited melanism in these moths by the action of chemicals. The only major criticism that can be brought against the experiments is that the results are too few to allow of statistical treatment, and therefore are not significant. But this criticism would bear more weight if the melanism had only appeared once in all the broods and moths dealt with. C. R. Plunkett<sup>1</sup> analyses Heslop Harrison and Garrett's results in detail and concludes that: "This work of Harrison and Garrett, if confirmed, is the clearest case yet adduced of the experimental induction of mutation and may throw light on an important factor in the mechanism of evolution." Heslop Harrison<sup>2</sup> later repeated the work using *Selenia bilunaria* and obtained similar results.

A. W. M. Hughes<sup>3</sup> repeated Heslop Harrison and Garrett's work on *Selenia bilunaria* on a rather more extensive scale, but he failed to obtain melanics. Thomsen and Lemcke<sup>4</sup> also attempted to induce melanism in this moth but their method of experiment was different from that of Heslop Harrison. In 1935 Heslop Harrison published results of further successful inductions of melanism in *Selenia* and he also showed that in all probability the work of Hughes and also of Thomsen and Lemcke were valueless for comparison with his own results, for their insects seem to have been riddled with disease. In Hughes's experiments there was a death rate of 88% in 23,760 eggs, in one case the death rate rose as high as 93.9%; and in Thomsen and Lemcke's experiments the lowest death rate was 70% and the highest 97.2%. It is well known that visible mutations are often deleterious, or at least constitutionally "weaker", than the normal animal. Accordingly, Harrison introduced a sporozoan disease into cultures of *Selenia* which would, under healthy conditions, be certain to produce melanics. The results showed that the disease caused a preferential elimination of melanics. There are

<sup>1</sup> 1927.

<sup>2</sup> 1928.

<sup>3</sup> 1932.

<sup>4</sup> 1933.

also several other legitimate criticisms which vitiate the work of Hughes and also that of Thomsen and Lemcke.

Other criticisms have been levelled at these experiments. For example, in spite of Heslop Harrison's warning about "latent genes" for melanism, Sonneborn<sup>1</sup> brought out such an explanation. Haldane, on the other hand, put forward the idea that, whereas the aberrant ratios in which the melanics first appeared tell against the idea of latent recessive genes, a hidden gene for melanism may have been linked to a lethal factor in the original broods. One may ask, if the melanic gene was hidden in this way why should it only become phenotypically expressed after treatment with chemicals? On *a priori* grounds we may expect that natural mutations will arise in organisms through chemical induction of some kind. There is, then, an *a priori* probability that Heslop Harrison's experiments point to a true induction of a mutation in the insects he used. Negative evidence has little bearing on the point at issue, unless the experiment is repeated by the same person, or if by someone else, then only when the original technique has been scrupulously followed and errors due to disease reduced to a minimum. Some confirmation, however, has been obtained from Walther<sup>2</sup>, who performed experiments similar to Heslop Harrison's, but who said he did not obtain any melanics. Heslop Harrison points out that in reality Walther did obtain such forms, and even described them without recognising that they were melanic forms.<sup>3</sup>

#### (b) *Mutations Induced by Heat*

Temperature is an ever-present environmental factor, which shows a fairly wide variation in different parts of the world, and from season to season in the same district. It is possible, therefore, that such a universal agent may play a part in the mutation process. Several geneticists, namely, Stadler<sup>4</sup> on barley and Muller<sup>5</sup> on *Drosophila*, however, have shown that changes of temperature do not necessarily alter the mutation rate induced by X-rays. Nevertheless, it has been shown by several other workers that under certain conditions temperature either induces mutations

<sup>1</sup> 1930.

<sup>2</sup> 1932.

<sup>3</sup> See Heslop Harrison, 1935, pp. 87-88.

<sup>4</sup> 1928b, 1930b.

<sup>5</sup> 1930b.

or at least increases the rate of their production. Muller and Altenburg in 1919 were the first to perform exact experiments of this kind on genetically known material. They submitted *Drosophila* to changes of temperature and obtained a definite but not statistically significant increase in the frequency of mutations. Later, Muller,<sup>1</sup> using a more refined technique, obtained positive results when *Drosophila* flies in the later imaginal and early larval stages were kept at 27°C. for 6-14 days, during the other stages they were kept at 19-20°C. Flies kept at the higher temperature showed a statistically significant increase of mutation frequency two to three times as great as that of the flies kept at the lower temperature. The intensity of the effect produced by temperature follows the relation  $Q_{10}=2$  to 3, that is, the rate of mutation is directly proportional to the temperature, and behaves in this respect like an ordinary chemical reaction.

Goldschmidt<sup>2</sup> and Jollos<sup>3</sup> both used a heat shock treatment on *Drosophila*, which had previously been used by Muller with slight, if any, positive response. Goldschmidt submitted larvæ to a sublethal temperature of 37°C. for 12 hours. These were then inbred for three generations, when many mutants appeared, indicating that mass mutation had occurred in the treated larvæ. Jollos, on the other hand, obtained different results. He submitted *Drosophila* larvæ to 37°C., a temperature which is just below the death point, for several successive generations, and found that a given gene mutated successively to a more and more intense allelomorphous expression. In other words, heat had a directive inducing effect on the mutation process. If this effect of heat were general it could be used to explain many small orthogenetic trends seen in organisms, such as the over-coiling of the *Gryphaea*, and which are difficult to explain on a selectionist basis.

However, neither Goldschmidt's nor Jollos' results have been confirmed. Plough and Ives<sup>4</sup> submitted six-day-old larvæ of five generations to 36°C. for 24 hours, dealing with some 200,000 insects. They found that the treatment increased the mutation rate by about six times the normal rate in control material, but no mass mutation was noticed, and the effect of the temperature was not orthogenetic. It can be concluded that, like X-ray and  $\gamma$ -ray

<sup>1</sup> 1928.

<sup>2</sup> 1929.

<sup>3</sup> 1934, 1935.

<sup>4</sup> 1934.

radiation,<sup>1</sup> heat does induce mutations, or increase the rate of natural mutation, but that none of these effects is at all sufficient to explain the natural process. Obviously other agents, internal or external, are in control of the mutation process. In some respects, indeed, the radiation and the temperature experiments lead to opposite conclusions about the nature of the mutations. This conclusion is discussed by Timofeeff-Ressovsky<sup>2</sup>, who points out that, as the spontaneous rate of mutation is directly proportional to the temperature, it would seem to be following the rules of "ordinary multimolecular chemical reactions", whereas the radiation experiments lead one to suppose that the mutation is concerned with a monomolecular reaction. Timofeeff-Ressovsky overcomes this apparent contradiction by assuming "that in the temperature experiments certain sources of mutation-inducing factors and not the mechanism of the mutation event itself (which is monomolecular) follow the Van't Hoff rule."

#### (c) Mutations Induced by Short Wave Radiations

Definite visible mutations by means of X-rays seem to have been first produced in work on the fungi. Nadson and Philipov,<sup>3</sup> working with species of the mould *Mucor*, produced some new strains which bred true for several generations. Later, in 1932-33, Dickson<sup>4</sup> produced several mutations by submitting the mould *Phycomyces Blakesleeana* and various species of *Chaetomium* to X-rays. He found that the older cultures mutated quicker than the younger ones, while the different species of *Chaetomium* mutated at different rates. The first inheritable mutations in the higher plants were produced by Stein who, in 1922, and later in 1932, submitted *Antirrhinum majus* to radium treatment and produced an abnormality which she called *Radiomorphose*. Some forms of this were not inherited, and others were. It now seems that the abnormality was due to a recessive gene mutation. But the real work on mutations induced by rays began in 1927, when Muller announced his spectacular successes in producing gene mutation in *Drosophila melanogaster* by means of X-rays.<sup>5</sup> The value of Muller's work over that of his predecessors who had attempted to produce mutations

<sup>1</sup> See following section.

<sup>2</sup> 1934b.

<sup>3</sup> Nadson, 1925; Nadson and Philipov, 1925.

<sup>4</sup> 1932.

<sup>5</sup> 1927b.

was that he planned it in such a way that detailed genetic analysis was possible, for the genetics of this fly was very well known by this time. Further, Muller and Altenburg<sup>1</sup> had been investigating the genetic behaviour of natural mutants for several years before he began to submit the flies to the influence of X-rays, and this experience enabled him to develop a technique for recognising sex-linked mutations by their breeding behaviour.

In his 1927 paper, Muller merely announced the results of his experiments, and gave some of the facts and conclusions to be drawn from them. The data and details of methods used were given in later papers. Muller found that, by treating the sperm of *Drosophila* with X-rays, he could induce true gene mutations; in fact, he says: "Several hundred mutants have been obtained in this way in a short time and considerably more than a hundred of the mutant genes have been followed through three, four or more generations. They are (nearly all of them, at any rate) stable in their inheritance and most of them behave in the manner typical of the Mendelian chromosomal mutant genes found in organisms generally."<sup>2</sup> In fact, the natural mutation rate was increased about 150 times by means of these rays. Many of the mutations produced artificially were the same as those which arise spontaneously in *Drosophila*, but others were new at the time; most of them were recessive, but a few were dominant; and most of them were lethal, at least when present in the homozygous state. Muller also found that X-rayed eggs of *Drosophila* gave rise to similar results.

There was little doubt now but that X-rays could stimulate the giving-off by the organism of constant mutations. So, from Muller's classic work there flowed much of our present-day knowledge of heredity and evolution. It also opened up the path to the preliminary investigations of the nature of the process of mutation and of the nature of the gene itself.<sup>3</sup>

Muller's claims have been well substantiated, particularly in *Drosophila*, to which insect most attention has been turned. Stadler<sup>4</sup> worked independently of Muller and published similar results obtained after exposing maize to the action of X-rays. Up to the present, some 64 different species of plants and animals have

<sup>1</sup> 1919.

<sup>2</sup> 1927b, p. 84.

<sup>3</sup> An account of Muller's technique for recognizing mutations and for measuring the mutation rate is given in the Appendix.

<sup>4</sup> 1928.



produced gene mutations when subjected to the action of X-rays. Timofeeff-Ressovsky<sup>1</sup> gives a list of 39 plants and 25 animals in which induced mutations have been found; in fact, all organisms to which these rays have been applied have responded positively. Among the animals which have mutated after X-ray treatment are *Drosophila*, silkworm,<sup>2</sup> mouse,<sup>3</sup> and parasitic wasps;<sup>4</sup> among the plants are *Datura*,<sup>5</sup> maize,<sup>6</sup> wheat,<sup>7</sup> barley,<sup>8</sup> cotton,<sup>9</sup> and tobacco.<sup>10</sup> All rays of different frequencies, i.e., of different degrees of "hardness", produce mutations. Other types of rays have also been applied to both plants and animals, and mutations have been reported.

Gager and Blakeslee<sup>11</sup> worked with *Datura* and produced results very shortly after Muller. They inserted tubes containing some radioactive substance into young buds of the plants and various kinds of mutations resulted; some of them were gene mutations which were brought forth apparently by the action of the rays on the sex cells in the developing ovaries in the buds. Buhholz and Blakeslee<sup>12</sup> also produced recessive gene mutations by exposing *Datura* pollen to the action of rays. In 1929 and 1933, Hanson and Heys showed that radium emanations produced lethal mutations in *Drosophila*, and the rate of mutation was found to vary according to the ionization of the air through which the rays passed. The same authors<sup>13</sup> also exposed the eggs of *Drosophila* to Y rays from polonium and found somatic mutations, but no genetic effects. Free electrons in the forms of cathode and Y rays from radioactive substances have also been tried, and successful results were obtained by Stadler<sup>14</sup>, who exposed barley to cathode rays from radiothorium; while Lindstrom<sup>15</sup> reported that Kopf produced a mutation in the tomato by the action of cathode rays.

<sup>1</sup> 1939.

<sup>2</sup> Astauroff, 1933.

<sup>3</sup> Dobrovolskaia-Zavadskaia, 1927 and 1928.

<sup>4</sup> Whiting, 1928, 1929 and 1932; Whiting and Bastian, 1931; Chalmers, 1930; Stancati, 1932; Greb, 1933.

<sup>5</sup> Blakeslee and collaborators, 1929.

<sup>6</sup> Stadler, 1928c, 1930.

<sup>7</sup> Delaunay, 1930; Sapéhin, 1930.

<sup>8</sup> Stadler, 1928.

<sup>9</sup> McKay and Goodspeed, 1930; Horlacher and Killough, 1931.

<sup>10</sup> Goodspeed and Olsen, 1928; Goodspeed, 1929.

<sup>11</sup> 1927.

<sup>12</sup> 1930.

<sup>13</sup> 1933b.

<sup>14</sup> 1931.

<sup>15</sup> 1933.

However, rays in the ultra-violet regions of the spectrum and beyond it seem to be mostly ineffective in producing mutations. But MacDougall<sup>1</sup> reports the production of mutations by ultra-violet light in *Chilodon uncinatus* (a protistan), while Stubbe<sup>2</sup> and Noethling<sup>3</sup> at first found no mutations after buds of *Antirrhinum majus* had been exposed to ultra-violet light, but treatment of the pollen by the rays seems to have been moderately effective. In *Drosophila* also, Altenburg<sup>4</sup> was unable to show that a definite increase in mutation rate occurred by the action of ultra-violet rays on the flies, but later<sup>5</sup> he irradiated adult flies, larvæ and eggs with ultra-violet and found that the eggs in a certain stage of development, when the germ track cells were near to the surface, showed a large increase in the mutation rate. An increase was not noticeable with the adults and larvæ. On the other hand, Rifenburgh<sup>6</sup> found that radiation of *Drosophila* eggs and larvæ by short wave light greatly increased the production of such non-heritable modifications as abnormal abdomen. The short waves also increased the frequency of crossing-over, particularly in the region of the spindle fibre attachment, but no mutations were recorded. It seems probable that with both  $\gamma$  rays and ultra-violet rays an experimental difficulty arises in the fact that much of the ray concerned is absorbed by the body tissues before it reaches the germ cells. In fact, Timofeeff-Ressovsky<sup>7</sup> has shown that the external body layers of *Drosophila* absorb practically all of the ultra-violet light applied. Providing that these difficulties of absorption and penetration can be overcome, ultra-violet light of different frequencies may allow us to investigate the nature of the mutation process by a study of the selective effect of different rays. Work on these lines has just begun, and Stadler and Sprague<sup>8</sup> have found that short ultra-violet waves produced mutations, whereas the long ones were ineffective.

So far as is known, white light, electricity, infra-red rays, and super-sonic rays have no mutational effects, at least on *Drosophila*. On the other hand, Jollos<sup>9</sup> considers that cosmic rays are probably effective.

<sup>1</sup> 1929 and 1931.

<sup>2</sup> 1932.

<sup>3</sup> 1934.

<sup>4</sup> 1928.

<sup>5</sup> 1933 and 1934.

<sup>6</sup> 1941.

<sup>7</sup> 1931.

<sup>8</sup> 1936.

<sup>9</sup> 1939.

Soon after the discovery of the effects of X-rays upon the mutation process of *Drosophila* the idea was put forward that perhaps spontaneous mutations owed their origin to the natural radiations of the earth's radioactive substances. For instance, in 1928, Olsen and Lewis<sup>1</sup> pointed out that the effect of natural radiation upon organisms should be tested. In 1929, Babcock and Collins<sup>2</sup> found a spot in a street tunnel where the intensity of natural radiation was twice as great as that in their laboratory. They then began to test the effect of the radiation in the tunnel on the production of mutations, and found that 2,500 tests made in the tunnel gave 0.52% of lethal mutations, while of the controls in their laboratory 3,481 tests gave 0.26% mutations. These results are not quite statistically significant, but nevertheless the authors considered them to be suggestive. Again, Hanson and Heys<sup>3</sup> found an abandoned carnotite mine in Western Colorado where the air was strongly ionized. After their experiments they found that 2,860 cultures of *Drosophila* in the mine gave 7 mutations equal to 0.245%, while the 1,308 controls in the laboratory produced one lethal mutation, a percentage of 0.076%. According to the authors, these results again are not quite statistically significant.

Other workers, including Muller, have also suggested that natural radiations are effective in producing mutations, until finally, Muller and Mott-Smith<sup>4</sup> published their statistical investigations in which they calculated the relation between the effects of natural and artificial radiation in order to obtain some measure of the frequencies of natural and artificially induced mutations. They took the lowest average spontaneous mutation value as given by several workers and found that the proportion of this to the highest induced mutation rate to be as 1 : 150, whereas the corresponding ratio for "natural" radiations was 1 : 200,000. This means that the spontaneous mutation rate is 1,300 times as high as that caused by natural radiations taken alone. Muller and Mott-Smith concluded "that natural radio-activity is not the major cause of mutations, and of organic evolution, but that most mutations come about as a result of other causes."<sup>5</sup>

An important conclusion which can be drawn from all of the work on induced mutations is that "agents which induce mutations

<sup>1</sup> 1928.

<sup>2</sup> 1929.

<sup>3</sup> 1930.

<sup>4</sup> 1930.

<sup>5</sup> 1930, p. 279.

lack specificity".<sup>1</sup> This means that the stimulus "producing" the mutation, such as radium, X-ray or temperature, does not determine the response of the organism; the latter reacts in its own way no matter what agent is used as a stimulus. There does not seem to be any constant behaviour among genes in different races and species, or between genes in a single species; even the different allelomorphic genes of a series mutate at different rates. For instance, the allelomorphs for the lighter eye colours of *Drosophila* have a higher mutation frequency than the darker allelomorphs,<sup>2</sup> or genes in different tissues may mutate at different rates. Under equivalent dosages of X-rays sperms seem to mutate more frequently than eggs in *Drosophila*.<sup>3</sup> The mutation rate is higher in older sperm than in younger, as Timofeeff-Ressovsky,<sup>4</sup> Harris<sup>5</sup> and others have found. Both of these writers have suggested that this is probably due to germinal selection of lethals in the young sperms. Demerec<sup>6</sup> has demonstrated the presence in *Drosophila virilis* of a number of recessive gene mutants which exist in several forms distinguishable only by their different mutation rates.

While the effect of the mutation stimulus (X-ray, etc.,) on the organism is indefinite it is not haphazard, but seems to be directional in some ways. This is indicated by the following experiments. Many mutants were known only in the heterozygous state, that is, the mutant gene was associated with a normal gene, as shown by the breeding behaviour. It has been found in fact that X-ray mutations are only concerned with one gene of a pair of chromosomes.<sup>7</sup> Again, several workers have shown that there is no genetic "after-effect" following X-ray radiation, or after introducing non-rayed chromosomes into rayed cytoplasm, for no mutations result. This shows that no secondary effects of radiation exist in the cytoplasm.<sup>8</sup>

For both X-rays and  $\gamma$ -rays a proportionality rule holds for the relation between the dosage of rays applied and the mutation frequency. The frequency is, in fact, linearly proportional to the amount of ionization produced by the rays (this can be conveniently measured in  $r$  or Röntgen units). The amount of ionization gives

<sup>1</sup> Just, 1932, p. 62.

<sup>2</sup> See Timofeeff-Ressovsky, 1932.

<sup>3</sup> Muller, 1929, and Hanson, 1935.

<sup>4</sup> 1931b.

<sup>5</sup> 1929.

<sup>6</sup> Various papers.

<sup>7</sup> Patterson and Muller, 1930, pp. 431-432.

<sup>8</sup> See Timofeeff-Ressovsky, 1934b.

an indication of the amount of energy received by the mutating gene. The linear proportionality rule was first demonstrated for X-rays and  $\gamma$ -rays by Hanson and Heys.<sup>1</sup> As the rule is true no matter what ray is used, it indicates that the effect of the ray is independent of the wave-length. This point and its implications in relation to the structure of the gene have been thoroughly examined by Timofeeff-Ressovsky, Zimmer and Delbruck.<sup>2</sup> They find that the mutation is produced by hits, possibly a single hit, which liberates energy and upsets the equilibrium within an atom of one of the molecules making up the chromosomes concerned. Equilibrium is restored by the rearrangement of the electronic or atomic structure of the atoms of the molecule. This rearrangement is the actual mutation. On this view a mutation is not the result of a destructive process, but is truly a change. In terms of evolution such gene changes could thus be expected to be more conservative agents than the more wholesale rearrangements of the chromosomes which are called chromosomal aberrations, or mutations. It is only an opinion, however.

## 2. GENE OR POINT MUTATIONS

The term mutation, as we have seen, implies the occurrence of a change of any magnitude in a species, but from a cytogenetic point of view it includes chromosomal mutations, such as chromosomal doubling or additions or subtractions of one or a few chromosomes from the whole complement, or purely genetic changes such as the alteration of a gene. In general discussions in the literature it is often difficult to tell to which type of mutations the writer is referring. We have already dealt with chromosomal mutations (see page 216) and shall now consider gene mutations, which some biologists believe to be of most importance in evolution, inasmuch as very slight mutations are said to satisfy the requirements of Darwinian theory.

Whatever a gene is, is not known; Mayr<sup>3</sup> remarks: "Even now we know very little about the nature of mutations, the term being merely a synonym for *X*, the unknown." Fundamentally, it means that, whatever it is that is situated at a certain locus of a particular chromosome and behaves in a certain way, suddenly begins

<sup>1</sup> 1929 and 1932.

<sup>2</sup> 1935, and see Goldschmidt, 1938, pp. 293-295.

<sup>3</sup> 1942, p. 67.

to behave in a different way. That many small changes in organisms used in experiment have been observed to follow Mendel's laws of segregation and recombination and act as recessives (usually) or dominants (uncommonly) has been known for some time. It was considered that this was sufficient justification for the geneticists to assume that such small changes were due to gene alterations. J. S. Huxley,<sup>1</sup> indeed, considers that all Mendelizing gene differences have arisen through mutation, because, as he says, "up to the present we know of no other way by which they could have come into existence." In practice gene mutations are identified when all possible mechanical chromosomal changes have been eliminated as the cause of the change, as Stadler<sup>2</sup> has emphasized.

After *Drosophila melanogaster* began to be used as a suitable subject for genetical investigations it was found that many of the mutations which occurred in the laboratory had their counterparts among wild populations of the flies. Indeed, it is generally true that natural mutations also arise under cultural conditions. Later H. A. and N. W. Timofeeff-Ressovsky,<sup>3</sup> Tschetverikov,<sup>4</sup> Dubinin and his collaborators,<sup>5</sup> Gershenon,<sup>6</sup> Gordon<sup>7</sup> and others began detailed genetical analyses of wild populations of various species and races of *Drosophila*. Sexton and Clark<sup>8</sup> also carried out similar investigations using the crustacean *Gammarus chevreuxi*. When *Drosophila* insects obtained from wild populations were bred in the laboratory in such a way that recessives could be extracted, it was found that the differences between the various races were gene differences affecting quantitative characters, similar to the usual mutations arising in old cultures. These workers found that in some cases different populations contained different concentrations of mutations. Some populations were found to contain similar mutations, others different ones, while even in the same population the concentrations of the types of mutations varied from year to year.

Gene mutations which are found to occur naturally are referred to as "spontaneous mutations". Because of their similar breeding

<sup>1</sup> 1942, p. 51.

<sup>2</sup> 1932.

<sup>3</sup> 1927.

<sup>4</sup> 1928.

<sup>5</sup> 1934, 1936, and 1937.

<sup>6</sup> 1934.

<sup>7</sup> 1935.

<sup>8</sup> 1936.

behaviour it is inferred that these natural variations are essentially similar to induced mutations. This may be so, but it is not really known whether or not the mutations are truly spontaneous, i.e., arise through some inherent change in the germ plasm, although this is commonly assumed. Navaschin<sup>1</sup>, for example, considers that the cause of mutation is purely internal to the cell. It is of course possible that the external environment may be responsible for the mutations. If this is so, artificially induced gene mutations would be not so much induced as their production rate accelerated by the stimuli applied.

Demerec<sup>2</sup> thinks that the most important property of the gene is its power of reproduction and that experiment shows that a gene can only stand slight changes because large ones destroy its reproductive power and so eliminate it. Hence large changes are of no use in evolution. But small gene changes have little effect on the organism. Because they are slight they will escape selection and so can accumulate until some kind of isolation may allow them to express themselves as new species. Such mutations, Demerec considers, are of great value in evolution. This, however, is a general assumption on which much of selection theory is built up.

In writing of the mutation theory Willis<sup>3</sup> states: "Since people wished to combine it with natural selection, they had to stipulate that mutations must be very small." Because the artificial gene mutations occurring most frequently are those with a scarcely perceptible effect, only recognizable by special methods, it is assumed that similar natural ones exist, and that evolution occurs through them. Baur,<sup>4</sup> who observed many small mutations affecting the flower shape in *Antirrhinum*, seems to have been the first to suggest this, and many others have adopted the idea because it fits in very well with the cytogenetics of varietal differences. Other workers have shown that these small gene mutations and those barely perceptible ones spoken of as "physiological mutations" have a much greater frequency of occurrence than the larger, easily seen and usually deleterious mutations, at least in *Drosophila*.

We have already shown that genetical theory depends on the existence of allelomorphs to the wild type genes. Each allelomorph is a mutant gene producing some change in the reaction system of

<sup>1</sup> 1933.

<sup>2</sup> 1935, p. 133.

<sup>3</sup> 1940, p. 43.

<sup>4</sup> 1924 and 1925.

the cell so that a new phenotype arises. Without this conception there would be no such thing as modern genetics. The gene mutations which are produced artificially behave in exactly the same way as those which are found in nature. Some act as dominants, some as recessives, multiple series have been found and so on. Many of the induced mutations are pleiotropic and have an effect on several characters, although the mutant gene is usually referred to according to the character it affects to the greatest extent. For example, the mutant gene "stubble" causes a shortening of the bristles in *Drosophila melanogaster*, but it also has an effect on viability, the legs, the antennæ and the wings.<sup>1</sup> Anatomy, morphology, etc., seem to indicate that evolution is irreversible and, as long as the presence-absence hypothesis of the gene was held, gene mutation also was regarded as irreversible. The Drosophilists, however, were soon able to show that reverse mutations, i.e., mutations from a mutant back to the original form, occur. To mention a few cases, O. Johnston and A. M. Winchester,<sup>2</sup> after exposing mutant *Drosophila*s to X-rays and mating with the original strains, found that the mutant genes *y* (yellow body colour), *sc* (scute bristles), *ct* (cut wings), *v* (vermillion), *f* (bristleless) and *m* (miniature wings) reverted back to their normal allelomorphs. Patterson and Muller<sup>3</sup> and Timofeeff-Ressovsky<sup>4</sup> have worked on these back mutations and one interesting case concerns the series of eye colours in *Drosophila melanogaster*. Here they found that the red wild type and other colours may mutate to white but white never mutates to red. However, white may mutate to eosin, and in the subsequent generation from this the eosin may produce red. The fact that the gene can become reversed renders it difficult to uphold the presence-absence theory, but at the same time, if the evidence from other branches of evolutionary biology is correct, this behaviour of the gene would seem to be running counter to the general rule.

In some cases mutations appear to be directive, but in the main they arise in all directions. It cannot be foretold which organ, tissue, or character is going to mutate; moreover, mutations are seemingly independent of the adaptive requirements of the organisms concerned. Hence it is often considered that the process of mutation occurs at random. Dobzhansky,<sup>5</sup> however,

<sup>1</sup> Dobzhansky, 1927 and 1930.

<sup>2</sup> 1934.

<sup>3</sup> 1930.

<sup>4</sup> 1931c.

<sup>5</sup> 1941, p. 37.



does not consider that this is altogether correct, for some genes are notoriously fickle, and mutate relatively frequently, whereas others have only been known to mutate once, and others not at all. Nabours,<sup>1</sup> for example, after studying the Grouse Locust intensively for about twenty years found only one mutation in all that time. It may be that very small or physiological mutations occur at random, but closer examination of the rather larger "ordinary" mutations is beginning to show that there is some order behind the process. There is some confusion on this point. For a given locus on a chromosome can indeed produce only a limited number of possible changes. This is to be expected on chemical grounds alone, for if a gene at a locus has a chemical nature, only a limited number of new chemical changes can arise. The organism, however, contains many different genes which, in respect of mutational behaviour, cannot be classed in any orderly way. Insufficient is known about the frequency and rate of mutation to be able to generalize about this matter. Even the total frequency of a single locus cannot be given, for we can never be sure whether or not all the mutations produced in a given time have been observed—some of them may be so small as to escape detection, but a few results of observations and experiments may be given.

Stadler<sup>2</sup> found a very great variation in the mutation frequency in maize (see Table 9). W. P. Spencer<sup>3</sup> spent eight years studying some 7,589 pedigree cultures of *Drosophila funebris* and *D. hydei* and including about 750,000 flies. It was found that the rate of spontaneous visible mutations varied greatly. For a continuous period of 38 months no mutations were observed.

Table 9.

*Gene Mutation Frequency in Maize*

Genes	R	I	P	Su	Y	Sh	Wx
Mutations per million gametes	492	106	11	2.4	2.2	1.2	0

Demerec<sup>4</sup> examined *Drosophila* flies from various situations as far apart as Florida and Japan and, grouping several genes together, he found a large variation in the number of lethals arising in the

<sup>1</sup> 1930, p. 351.

<sup>2</sup> See Waddington, 1939, p. 381, after Stadler.

<sup>3</sup> 1935.

<sup>4</sup> 1937.

chromosomes. The number of chromosomes tested in each strain varied from 3,049 to 545, and the number of lethals found varied from 28-0 with the majority from 2-0. In one individual case 2,108 chromosomes were found to produce 23 lethals, but in another 3,049 chromosomes had only 2 lethals, and in a third 1,236 chromosomes produced no lethals. Timofeeff-Ressovsky<sup>1</sup> X-rayed an American and a Russian race of *Drosophila melanogaster* and found that, in a given time, the American race produced 55 mutations from red to white eye involving 59,200 flies, while in the same time the Russian race produced only 40 similar mutations involving 75,300 flies. The same author,<sup>2</sup> considering the lethal genes of *Drosophila* as a group, estimates that in every generation one of the chromosomes produces a new lethal in 1% of cases. J. S. Huxley<sup>3</sup> thinks that a general mutation rate of 1 in 10<sup>5</sup> or 1 in 10<sup>6</sup> may be expected. This is about the mutation rate of *Drosophila*. The rate of mutation in different organisms must in fact vary considerably, otherwise on the basis of the number of lethals produced by *Drosophila* in its short lifetime of a very few weeks, an ordinary mammal or other long-lived creature "would be riddled with lethals in a few generations," as Dobzhansky<sup>4</sup> says.

Further, it is universally acknowledged that the vast majority of visible mutations, especially induced ones, are, if not actually lethal, generally deleterious to the organism. For instance, Robson and Richards<sup>5</sup> find that out of a list of 389 types of mutants given by Morgan, Bridges and Sturtevant,<sup>6</sup> 210 of them are either directly lethal or defective enough to be classed almost as lethal. Hence, experimentally, gene mutation is a negative process reducing viability.

It is not easy to understand how a predominantly negative process in the organism can be of great value to the progressive process of evolution of the species. It is, however, generally said to be expected on *a priori* grounds that the mass of mutants is deleterious because a mutation is an untried change interpolated into a tried and successful system. The suggestion is, then, that mutations are accidents due to some temporary or local upset in the metabolic machinery,

<sup>1</sup> 1932.

<sup>2</sup> 1937.

<sup>3</sup> 1942.

<sup>4</sup> 1941, p. 37.

<sup>5</sup> 1936, p. 222.

<sup>6</sup> 1925.

or developmental processes in the germ plasm. In fact, we may say that the appearance of a mutant may be the outward sign of the struggle of the organism to maintain its good health. If this is so, then the fact that new phenotypes arise also seems to be of little consequence to the species as species, for the phenotypes may be the mere accompaniments of pathological changes. Robson and Richards<sup>1</sup> have argued these and similar points well, and they put the matter tersely by saying: "It is possible that we ought rather to say that even the pathological mutations of *Drosophila* produce visible structural variations." What, then, is the value of small mutations of rare occurrence in the long-term process of evolution?

There are examples of mutants which, under ordinary conditions, are viable but which under slightly different conditions become even more adapted to the environment than the original parent organism. For instance, Timofeeff-Ressovsky<sup>2</sup> found that the viability of a mutant of *Drosophila funebris* varied with the temperature until at 24-25°C. it was superior to that of the wild type. We should note here that the viability was tested under the unnatural conditions in which *Drosophila* was cultured in the laboratory. Another example is given by Banta and Wood,<sup>3</sup> who found a thermal race of *Daphnia longispina* which apparently originated as a recessive mutation from the normal flea. It was able to survive temperatures as much as 7°C. higher than the normal *Daphnias*. Different behaviours of this kind are physiological in nature, hence "physiological mutations" may be of some importance.

Further, the mathematical selectionists have calculated that the rate of production of viable mutations is far below that necessary to allow for any significant evolutionary change by means of them. For instance, Fisher<sup>4</sup> states that: "The frequency of individual mutations in *Drosophila* is certainly seldom greater than one in 10,000 individuals, and we may take this figure to illustrate the inefficacy of any agency, which merely controls the predominant direction of mutation, to determine the predominant direction of evolutionary change. For, even if selective survival were totally absent, a lapse of time of the order of 100,000 generations would be required to produce an important change with respect to the

<sup>1</sup> 1936, p. 220.

<sup>2</sup> 1934c.

<sup>3</sup> 1927 and 1939.

<sup>4</sup> 1930, p. 19.

factor concerned, in the heritable nature of the species. Moreover, if the mutant gene were opposed, even by a very minute selective disadvantage, the change would be brought to a standstill at a very early stage." In order to overcome this very real difficulty of the sheer lack of mutations suitable for evolutionary changes, R. A. Fisher brought forward his theory of dominance.<sup>1</sup> Let us state the argument behind this theory briefly. The majority of mutants when they arise are present in the heterozygous state. Those that tend to be dominant—that is, those that tend to produce definite phenotypic effects—will be adversely selected. But as most mutations are produced repeatedly, the presence of genes modifying the expression of the mutant will be advantageous to the organism. In the course of time it can be expected that the mutant gene will become pushed into recessivity by the selection of subsidiary genes modifying it. Hence the theory of dominance depends on a selection of the environment of a mutant gene so as to prevent it from producing a bad effect on the mutants organism. Evidence for the theory is derived from the known reaction between genes; there are many known cases in which certain genes reduce the dominance of other genes.

This theory has been drastically criticized by Wright<sup>2</sup> and by Haldane,<sup>3</sup> for it implies that for every new mutant gene produced several subsidiary ones must sooner or later arise, too. These subsidiary genes must also be suppressed by others, and so on *ad infinitum*. The theory obviously does not overcome the difficulty it is meant to solve. It does not enable us to see how rare beneficial mutations have brought about the evolution of species. Instead, it only complicates still further a mechanism already overburdened with far too many cogs.

E. M. East<sup>4</sup> tackles the problem in another way. He recognises that, unless we assume evolution has now ceased altogether, higher mutation rates than those known already, and also mutations of a different kind than the usual type, are necessary to allow evolution to proceed. The mutations which he has in mind are those which alter the developmental activity of the organism from the beginning by changing its pattern. He suggests that constructive mutations of this type are in fact quite numerous, but are usually overlooked

<sup>1</sup> Fisher, 1928, 1931, 1934; Ford, 1930.

<sup>2</sup> 1929.

<sup>3</sup> 1930b.

<sup>4</sup> 1935 and 1936.

in favour of the lethal and sub-lethal types. We know from experience that variation in nature, especially of quantitative characters, is great; in genetical terms, the mutations required for evolution are those which work cumulatively in a system of multiple allelomorphs. East has clearly returned to the original Darwinian view, and, indeed, in his first paper he concludes by saying: "*The deviations forming the fundamental material of evolution are the small variations of Darwin.*" This conclusion follows as a matter of course. We return to the Darwinian idea, modified by the demonstration of alternative inheritance."<sup>1</sup>

Dobzhansky<sup>2</sup> attacks these difficulties in another way on the ground that anthropomorphic conceptions of what are harmful or useful characters in an organism may be without foundation in nature. A few workers have shown that the environment may affect the viability of some mutations. This does not mean that the viability of all mutations is dependent on the surroundings.

Sturtevant<sup>3</sup> considers that, as a relaxation of selection in nature leads to deterioration of the stock, and as this deterioration is increased by inbreeding, it may be that, under artificial conditions, the general mutation rate is raised. He also asks: "Are all mutation rates so far determined experimentally too high to be applicable to natural populations?" He points out, further, that if the mutation rate in a species fell to zero it would be fatal to it, for it would not then be able to adjust itself to a changing environment. This leads to a question. Why does not the mutation rate actually fall to zero in nature when the deleterious mutations so vastly outnumber useful ones? Sturtevant<sup>4</sup> says: "No answer seems possible at present, other than the surmise that the nature of genes does not permit such a reduction. In short, mutations are accidents, and accidents will happen."

Without going any further into the question of the value of gene mutations to the species, it is enough to remark that the whole subject bristles with difficulties. In spite of these difficulties, the neo-Darwinians have seized on gene mutations, especially those kinds which are scarcely recognizable, as by far the chief (if not the sole) means whereby evolution occurs.

We need to state that gene mutations, if they are the raw

<sup>1</sup> 1935, p. 450.

<sup>2</sup> 1941.

<sup>3</sup> 1937, p. 465.

<sup>4</sup> 1937, p. 466.

material of evolution, do not act alone, but in conjunction with natural selection. Timofeeff-Ressovsky<sup>1</sup> distinguishes three basic mechanisms which alter the genetic make-up of a population. These are the mutation-pressure, selection pressure and the limitations of population size. Mutations by themselves are non-directive because they arise at random and the rate of their production is so slow. The directive factors are selection and isolation; the one keeps the organism in good relations with the environment, while the other concerns its spatial relationship. Of these factors, Timofeeff-Ressovsky considers that mutation and population waves supply the raw material of evolution, while selection and isolation control its course. Size of population will affect the evolution of species through the agency of mutant genes, because the smaller the population the greater the chances of spread due to what is called "drift", but the lesser the chances of causing significant variations due to the lack of possible combinations among the few members of the population available. On the other hand, in a large population there will be many more mutants with greater possibilities of affecting evolution through the increased chances of making new combinations. Finally, Sewall Wright<sup>2</sup> points out that in a large population, where interbreeding is free and where no changes of conditions occur, gene frequencies will approach equilibrium values dominated by selection. When the population has reached a certain stage in its relation to its environment no further evolution will occur in spite of mutation, variability and selection. For further evolution to take place the environment must be altered. Accordingly, Wright considers that one of the most important causes of evolution lies in repeated changes in the environment of the evolving organisms.

### 3. NATURAL SELECTION

#### (a) *General Account*

Biological investigations since the time of Darwin have produced a revolution in the interpretation of the idea of natural selection. In Darwinian days, natural selection was considered to be the causal creative agent in evolution; it worked by choosing the continuously arising fit varieties. In Darwin's time, it followed

<sup>1</sup> In *New Systematics*, ed. J. S. Huxley, 1940, pp. 121-122.

<sup>2</sup> *ibid.*, p. 174.

from the theory of blended inheritance, hence it was necessary that these varieties had to arise continuously. But the genetical investigations of Morgan and many others, which led to the formulation of the theory of the gene, indicated that heredity could also act as a stabilizing force. In evolutionary investigations the emphasis was then moved from consideration of external environmental agents to that of the controlling factors in the internal environment. The creative force was seen to lie in the production of mutations; selection then fell naturally enough into the secondary rôle of guiding the species safely along a path predetermined by the nature of the mutations that arose.

The theory of natural selection, as Dobzhansky<sup>1</sup> points out, is essentially a theory of the origin of adaptations, and only secondarily a theory of evolutionary causation. The neo-Darwinians, however, equate the phenomena of adaptation and evolution, inasmuch as they consider that a demonstration of the way in which an organism has become adapted to its environment furnishes evidence of the way in which the organism has evolved. Most demonstrations of this kind are concerned with macroscopic differences of structure, such as differences of colour, size and so on. Yet in their theoretical discussions based on cytogenetics and mutation theory the same neo-Darwinians are led to consider the extremely small variations, with little, if any, visible effect, as the raw material of evolution on which natural selection works, whereas the large visible mutations are said to be of little use in evolution. But biological opinion is by no means unanimous about these matters, and probably the root of the difficulties involved in the idea of natural selection, considered in relation to the origin of adaptations and to evolution, lies in the fact that experimental investigations of the subject encounter unsurmountable obstacles due to the very complex circumstances in which living organisms live and have their being. Unlike the problems of physics and chemistry, the problems of biology, and particularly of evolutionary biology, can never be completely understood without reference to the environment, and this includes the whole of nature, with its almost infinite number of variables.

Up to this point our accounts of natural selection doctrine have been largely theoretical, but this is inevitable, for, like the Lamarckian doctrine, there is a paucity of experimental evidence in favour of the idea. In this section an account of the evidence for and

<sup>1</sup> 1941, p. 187.

against the actual operation of selection in nature is given. If natural selection is a causal agent in evolution, it becomes necessary to show that this agent has changed a variety or species, and to do this involves certain logical requirements, which have recently been listed by Pearl.<sup>1</sup>

“ 1. *Proof of somatic differences between survivors and eliminated*

This is the first logical step in the demonstration of the action of natural selection in a particular case.

2. *Proof of genetic differences between survivors and eliminated*

No proof of the effectiveness of natural selection in altering a race can be logically complete until it has been demonstrated that there are genetic differences between survivors and eliminated as well as somatic differences.

3. *Proof of effective time of elimination*

It may be said that to establish a logically complete demonstration of the effective action of natural selection it is necessary to have careful regard for the age of eliminated and surviving individuals in relation to their periods of reproduction, in order to be sure that otherwise selective deaths occurred at an age such that they could have affected the race.

4. *Proof of somatic alteration of a race*

It must be shown by adequate biometrical investigation that the race in question is somatically different after the particular event of selection, or after the lapse of a reasonable secular period in the case of continuing selection from what it was before.

5. *Proof of genetic alteration of a race*

It is still necessary to show that the race following a particular act of selection, or after a reasonable secular period in the case of continuing selection, is *genetically* different from what it was before the selection, if proof is to be complete.”

As far as we know, no single investigation of a particular case of natural selection has fulfilled all of these requirements, and most of them have only satisfied one, or perhaps two, of them. A complete experimental demonstration that natural selection is a factor in evolution is therefore wanting. Thus, Robson and

<sup>1</sup> 1930.



Richards<sup>1</sup> can say: "We do not believe that natural selection can be disregarded as a possible factor in evolution. Nevertheless, there is so little positive evidence in its favour, so much that appears to tell against it, and so much that is as yet inconclusive, that we have no right to assign to it the main causative rôle in evolution." While Fisher,<sup>2</sup> the mathematical selectionist, can only remark: "Although it appears impossible to conceive that the detailed action of Natural Selection could ever be brought completely within human knowledge, direct observational methods may yet determine numerical values which condition the survival and progress of particular species."

(b) *Evidence for the Occurrence of Natural Selection*

Evidence for the occurrence of natural selection is obtained from many sources. Some of it is direct and concerns observations made on organisms in their natural habitats, some of it is indirect but based on experiments performed in the laboratory. Much of the evidence is presumptive, or indirect, based on considerations of the adaptations of organisms to their environment, the assumption here being that, unless we grant natural selection as the force directing the attainment of the adaptation, we are unable to explain it. Under this heading come all those cases of mimicry, warning coloration, protective resemblance and special adaptations to special habitats such as the deeper regions of seas, or swiftly flowing mountain torrents and so on. The aim of most of the actual work done on natural selection is to show that a differential death-rate in nature or in experiment is due to a selective process. Clearly the mere demonstration that selection acts in nature does not cover the requirements of a proof that natural selection is an evolutionary agent as demanded by Pearl.<sup>3</sup>

(i) *Miscellaneous Direct Observational and Experimental Presumptive Evidence in Favour of Natural Selection*

There are really few direct observational or laboratory experimental cases which have been advanced as evidence for the

<sup>1</sup> 1936, p. 316.

<sup>2</sup> 1930, p. 47.

<sup>3</sup> Accounts of the modern evidence for natural selection are given in Robson & Richards' *Variation in Animals in Nature* (1936), in *The New Systematics*, ed. by Julian Huxley (1940), and Julian Huxley's *Evolution, The Modern Synthesis* (1942). We have already mentioned the earlier similar treatments of natural selection of Kellogg (1907) and Plate (1903).

occurrence of natural selection. Of those cases mentioned under the above heading some are direct observations of organisms and changes in those organisms under natural conditions, whereas others are experimental in the sense that they were performed in the laboratory. It may be said that any selection observed under experimental conditions is artificial and bears no relation to selection in the wild state. This is true to a certain extent, but it does not really vitiate the purpose of the experiment, which is to find out whether or not any kind of selection, excluding that practised by man, is effective in producing a differential death rate and altering the expression of a character within a population.

Some more or less direct accounts of changes in whole populations over a period of years have been given, from which it has been inferred that natural selection is the agent responsible for the changes. For instance, the melanic form of the peppered moth (*Amphidasys betularia*) was first found in the Manchester area in 1850 and it has now supplanted the original non-melanic form in many places. The diurnal butterfly *Heodes phlaeas* L. has a very wide distribution extending over most of the northern hemisphere, but the race inhabiting only Madeira shows little affinity with other geographical races. Ford<sup>1</sup> examined the collections of Wollaston, and, on comparing them with his own specimens, caught about seventy or eighty years later, found that there were slight but definite differences in the populations.

Again, Ford<sup>2</sup> also gives a remarkable example of variation in a population of the marsh fritillary (*Euphydryas aurinia*) occurring in Cumberland. We quote the relevant paragraph: "The species was quite common in 1881, and gradually increased until by 1894 it had become exceedingly abundant. After 1897 the numbers began to decline, and from 1906 to 1912 it was quite scarce. From 1913 to 1919 it was very rare, so that a few specimens only could be caught each year as a result of long-continued search, where once they were to be seen in thousands. From 1920 to 1926 the butterfly had become excessively common, and so it remained until we ceased our observations in 1935." When the population was small, variation was low and the population consisted practically of a constant form; when the population was large variation was extreme. Ford infers that the environment determines the size of the population and that, in consequence, when it is small selection will

<sup>1</sup> 1923-24.

<sup>2</sup> 1945, pp. 268-270.

be intense and variation will be at a minimum; but when the population is large and the environment is favourable he considers that selection will be weak and so variation would be expected to be at a maximum.

Accounts of four different approaches to the problem of natural selection are given below in some detail. They represent the better type of investigation of a more or less direct kind carried out up to the present. They indicate that selection is an actual process in nature and they point the way to the method by which natural selection aids the evolutionary process.

( $\alpha$ ) *Crampton on Selective Elimination in Philosamia*

Crampton<sup>1</sup> explains the purpose of his researches in the introduction to his paper where he writes:<sup>2</sup> "The following account is a statement of the results of an examination into the occurrence of 'natural selection' in the case of over-wintering pupæ of *Philosamia cynthia* as this species occurred in New York City in the year 1899. It is concerned, therefore, with the existence of a definite relation between elimination on the one hand, and the extent and character of variation on the other; and particular attention is directed towards ascertaining the real basis for the selective process." In particular he notices that large numbers of pupæ of the Ailanthus silk-worm, *Philosamia cynthia*, found in nature were dead or deformed, and he attempted to find out the causes of this elimination.

Crampton collected 1,090 cocoons and found that 55 contained dead and shrunken pupæ; 84 were empty cases from which the moths had escaped; 9 were cocoons containing an adult insect which had been unable to emerge from the pupa case; 623 contained fully formed pupæ but they were dead; finally 319 normal pupæ were left to continue the race. But of these 319 pupæ, 97 males and 84 females gave rise to insects among which 38 were greatly deformed; 75 were slightly deformed; 16 did not reach maturity; the remainder, 52 in number, or 4.8% of the total number of cocoons, produced perfect imagos. Truly the death rate was amazing!

Next, Crampton attempted to see whether or not elimination of the pupæ was selective or haphazard. For living and dead pupæ he measured (a) total lengths, (b) total weights, (c) length

<sup>1</sup> 1904.

<sup>2</sup> 1904, p. 114.

of bust, (d) width of bust, (e) dorso-ventral depth of bust, (f) length of left antenna and (g) breadth of left antenna. He analysed the results statistically and found that for pupal elimination there was significant evidence of selection. Six of the characters in the surviving males differed in measurements from those of the eliminated males. The surviving females differed in all characters from those of the females which perished. The type of selection of both male and female was in the same direction. At the time of metamorphosis there was evidence to show that more females were eliminated than males.

Extending his conclusions Crampton<sup>1</sup> states: "*Nevertheless the fact of primary importance is, not that selection is here natural in the sense that it would have occurred in nature, but that the reduction in numbers proceeds hand in hand with a restriction in certain structural characteristics as regards type and variability.*" Crampton, however, does not fall into the error of assuming that because a surviving insect possesses certain types of characters those are the "cause" of its survival; rather does he incline to the view that possession of certain combinations of characters renders the insect "fitter" to survive than those insects which depart from the type. Total "fitness" is dependent upon the proper co-ordination of both structural and functional characters. So Crampton concludes "that the test of fitness or unfitness has reference to the physiological and morphological co-ordination or correlation among the constituent elements of the whole organism, and that any relaxation in either series, in a formative sense or otherwise, results in an instability which may culminate in death and which expresses itself in structural deviation as well as in a higher degree of variability."

( $\beta$ ) *Heslop Harrison on the Evolution of Local Races of Oporabia autumnata*

Some parts of the observations of *Oporabia autumnata* made by Heslop Harrison<sup>2</sup> furnish another example of local and distinct changes in populations occurring over a short period of time, and other parts of them show the effect of natural selection on existing varieties of local races in different habitats.

Eston Moor lies in the Cleveland district of Yorkshire. Ever since the Middle Ages attempts have been made to turn the land to agricultural use, leaving some areas as common grounds. The

<sup>1</sup> 1904, p. 129.

<sup>2</sup> 1920.

moth *Oporabia autumnata* apparently ranged over the whole moor wherever the suitable food plants occurred, but by the year 1800 a change in the arboreous composition set in, breaking up the moor into distinct regions. By 1860, an eastern region called Wilton Wood and a western portion called Normanby Intake Plantation were recognised; both were mainly coniferous but had clumps of birch and alder. These woods were separated by an area of heather and bracken a half-mile in extent. The moths were confined to the woody areas because they feed on birch or alder. In 1885 a heavy gale destroyed many trees in the Intake Plantation and those undamaged were cut down. Heslop Harrison visited this plantation in 1906 and found it occupied by birch saplings and only a few coniferous trees, and again in 1919, by which time birch was completely dominant. On the other hand, Wilton Wood remained as a coniferous wood in which the few remaining birches and alders were gradually disappearing.

Hence from 1885 onwards the local colonies of *Oporabia autumnata* were forced to live in two unlike woods in one of which larch was the chief food plant while in the other birch was the food plant. Along with the vegetational changes in the area Heslop Harrison found in the moth species corresponding evolutionary changes which must have occurred since 1885. The mean size of the local race in each wood had altered, the Wilton Wood moth had become duller and only feebly marked, with a small range of colour variation, while the Intake Plantation moth had developed a much bigger range of variation producing many silvery forms, and finally, a change in the time of emergence of the imago from the pupæ of the insects in the woods was noticed.

Heslop Harrison sought an explanation from the changes which had taken place in the woody composition of the area. He<sup>1</sup> states: "In investigating the change in the modal state of the wing pattern one must guard against the assumption that any extension of the range of normal variation has occurred; what has happened, in reality, is a very definite contraction of that range of such intensity as to throw the modal condition into a position giving the two local races facies so diverse as to suggest an apparent discontinuity. This, examination proves not to occur, for the alteration in mean proceeds directly from a preferential preservation of the darker, suffused, feebly marked forms and an accompanying elimination."

Apparently some factor is causing selective elimination of the

<sup>1</sup> 1920, p. 223.

higher coloured forms in the dark coniferous wood. In the birch wood, although all silvery ones blend better with the trees, all these insects are conspicuous; but bird life barely exists. In the larch wood, however, the dark forms blend better with the dark coloured trees; birds abound in this wood. Heslop Harrison has, however, made observations in day time over many years and has never seen one *Oporabia* insect of any colour attacked by a bird. He then considered the vulnerability of *Oporabias* in the coniferous wood at night, or at dusk, when owls, nightjars and bats might prey on them. He thought that the brighter coloured *Oporabias* might be preferentially selected as food by these animals. He then collected as many forewings (which are not eaten by the animals) as possible from the ground in the wood. In all, he obtained 17, and found that two of these were dark in colour and showed evidence that spiders had been the predators. Of the other 15 the majority were silvery in colour. This preponderance was all the more significant as it occurred in a population where the darker forms outnumbered the lighter ones in the proportion of 25 : 1. Heslop Harrison<sup>1</sup> states: "This cannot be a mere matter of chance; selection must be at work—and natural selection carried out by bats, owls and nightjars. . . . In my opinion, therefore, it is to natural selection, carried on by nocturnal birds in company with bats, we have to look to explain the rapid change in average condition the insect has displayed in the Pinewood."

(γ) *Quayle on the Effects of Fumigation on Scale Insects*

By distributional and experimental studies Quayle<sup>2</sup> and his collaborators have shown how selection may act on wild populations of insect pests.

The citrus groves of the western seaboard states of America are subject to the ravages of various *Coccidae*, or scale insects. Sprays of hydrocyanic acid have proved very effective in controlling their ravages. As early as 1914 Melander put forward evidence to show that scale insects were capable of developing a certain immunity to these sprays. In 1914 also, Quayle found that, in spite of regular fumigation with hydrocyanic acid, the red scale (*Aonidiella aurantii*, Mask.) was still abundant in certain citrus orchards of the Corona district of California. In neighbouring

<sup>1</sup> 1920, pp. 224-225.

<sup>2</sup> 1938.

districts fumigation had been successful. This condition of resistance in the insects has persisted up to at least 1937 and has spread to other districts.

Quayle<sup>1</sup> and Lindgren<sup>2</sup> and several other workers then began comparative investigations of resistance to this poison of red scale insects obtained from different localities. It became evident that two races or types of red scale existed; one of them is resistant to fumigation by hydrocyanic acid and the other one is not. Quayle and Lindgren cultured resistant and non-resistant red scale insects on banana squash in insect-proof rooms, and subjected them to different dosages of fumigant. By the time of publication four generations of insects had been obtained, and the difference in resistance between the two types of insects was maintained. Experiments also showed that the resistant type of red scale displays an increased immunity to other insecticides, such as carbon disulphide, methyl bromide and ethylene oxide. This behaviour of the insects indicated that the resistance developed by the resistant type of insect may be due to some fundamental change. And, indeed, the relative immunity is inherited, for Dickson<sup>3</sup> later showed, by means of crossing experiments, that the  $F_1$  hybrid between resistant and non-resistant insects is intermediate in respect to immunity and is controlled by a sex-linked factor.

Resistant races of other scale insects are also known. In 1912, Woghum found a resistant strain of the black scale insect (*Saissetia oleæ* Bern), which arose spontaneously in a district of Los Angeles; by 1925 it had spread to an area of 40 miles extending from the place of origin. Gray and Kirkpatrick<sup>4</sup> have shown experimentally that two races of these insects, one relatively resistant to hydrocyanic acid, the other non-resistant, exist in nature. Again, in 1925, Quayle found a resistant type of the citricola scale insect (*Coccus pseudomagnoliarum* Kuw.) in a localised area in California. The resistant type spread very rapidly, and in about four years it had occupied most of southern California. This resistant type continued to infest the orange groves until 1933-34, when it disappeared through natural causes.

This work on citrus scale insects thus represents an extensive investigation, in the field and in the laboratory, of the physiology,

<sup>1</sup> 1938.

<sup>2</sup> 1938.

<sup>3</sup> 1940.

<sup>4</sup> 1929 a and b.

genetics and distribution of resistance in the resistant types of the insect. It is assumed by Quayle that the resistant type arises by a gene mutation, and he considers that: "The greater tolerance resistance of HCN fumigation that has developed in three of the most important citrus scale insects in certain localities in California has been brought about, apparently, through natural selection."<sup>1</sup> We may conclude that natural selection may provide an explanation of the rapid rise and spread of the resistant insects, because, due to the method used in the control of these scale pests, there might have been an intense differential selection of any resistant strain that appeared. The evidence proved by the history of the spread of the resistant red and black scale insects may provide support for the theory that the resistance spread from an original focus.

(δ) *Popham on the Variation of Colour in Arctocoris*

While collecting insects from ponds Popham<sup>2</sup> noticed that the colour of most species of *Corixa* (water-boatman) matched that of their background. He thereupon attempted to estimate the significance of colour variation of those insects when exposed to predators under conditions closely resembling those in nature. He measured colour variation of the insects and of the background by a standard Ostwald colour chart which consisted of a series of grey colours, each one differing from its neighbour by the same apparent contrast. As insects and the background on which they were kept were both coloured brown, the charts used expressed the grey value of the colours of the insects. One series of experiments showed that the species of a water-boatman are at ease on a background of the same or similar colour to themselves, but on a differently coloured background they become restless and attempt to fly away.

The insect used in the experiment was *Arctocoris distincta* which spends most of its time at the bottom of the pond, only coming to the surface occasionally to breathe. The predator used was the Rudd (*Leuciscus erythrophthalmus*). The tanks used in the experiments measured 36" x 15" and they contained water to a depth of 2½ inches with a substratum of mixtures of cement and sand, of silver sand, of two different sands, or of emery powder. These substrata gave colour values described by the letters *a*, *c*, *e*, *g*, *i*, *l*, and *n*. In each experiment three fishes each three inches long

<sup>1</sup> 1938, p. 207; see also Dobzhansky (1941).

<sup>2</sup> 1941.



were put into a tank and shortly afterwards the insects were let in gently. Whenever an insect was eaten or wounded another of the same colour was added, thus keeping the population constant.

In one experiment equal numbers of insects of two different colour values, *i* and *l*, were put in a tank with the background colour value *i*. The insects with the colour value *i* may then be said to be "protected" while those with the colour value *l* are "un-protected". It was found that the Rudds killed twice as many non-protected as protected insects. In another set of experiments three types of insects with the colour values *n*, *l* and *i* were used collectively on a variety of contrasting backgrounds, with colour values *a*, *c*, *e*, *l* and *g*. The results are shown in Table 10; they indicate that there is a certain variation in the intensity of selection of the insects by the fishes.

Table 10  
*Results of one of Popham's Experiments*

Colour of background	Colour type of insect and percentage of each destroyed		
	<i>i</i>	<i>l</i>	<i>n</i>
<i>a</i>	33	34	33
<i>c</i>	26	38	36
<i>e</i>	27	32	41
<i>g</i>	11	36	53

In other experiments Popham obtained results which showed that the discriminatory powers of the Rudd to choose the less protected (the less adapted) prey were decreased by lowering the light intensity, by increasing the number of predators used, by decreasing the concentration of numbers of the prey available, by using insects with a slight colour difference or by using insects with a relatively very large colour difference. Again, by using different species of *Arctocorisa* he found that the predators discriminated between the sizes of the prey, choosing only those of an intermediate size, neither very small, nor very large.

Popham concluded that the adaptive coloration of this insect, the water-boatman, has a certain selective value against certain backgrounds. Natural selection tends to exterminate the misfits at a greater rate than those insects better adapted to the environment.

But selection is not the only factor at work in this process, for the discriminatory powers of the predators vary according to circumstances determined by temperature, concentration of the populations of both prey and predators, etc. Indeed, the results of Popham's one set of experiments "show how a small proportion of an animal population may survive the destructive activities of predators, whether or not the minority be less adapted to that environment than those which occur in larger numbers."<sup>1</sup>

(ii) *Indirect Evidence for Natural Selection*

Circumstantial evidence for natural selection is provided by examples in the natural world showing that certain adaptations make an organism better fitted for survival in certain habitats than those organisms without the adaptations.

(α) *Miscellaneous Examples*

In 1930, Todd reported the effects of selection on *Streptococcus haemolyticus*, the microbe which causes scarlet fever, and puerperal fever. If this organism is grown on agar it very soon loses its virulence and powers of infecting animals. Todd discovered that the organism produces hydrogen peroxide and when grown in agar cultures, this substance is toxic to it. Mutations, however, arise which do not produce hydrogen peroxide, or at least much less of it than the normal strain, and so the mutants are enabled to live on agar. These mutants are also less virulent in animals. Here, then, we have an experimental example of selection choosing the less virulent type of a facultatively parasitic organism, which does not produce hydrogen peroxide, at the expense of the more virulent form.

L'Héritier and Teissier<sup>2</sup> cultured mixtures of various types of *Drosophila* mutants in known proportions and obtained results indicative of the survival value of the mutants. For instance, they found that in a mixture of normal winged and vestigial winged *Drosophilas* exposed to the influence of wind, the proportion of vestigial increases, whereas in a mixture of normal flies with the bar eye mutant, the proportion of the latter decreased. Again, an experiment with a mixture of normal *Drosophilas*, the ebony mutant and the natural hybrids between them showed that the hybrid form possessed some adaptive advantage which was greater

<sup>1</sup> Popham, 1941, p. 151.

<sup>2</sup> 1934 and 1937.

than that possessed by either of the two homozygotes. Spencer<sup>1</sup> has also found that under normal conditions vestigial winged *Drosophilas* are less viable than the normal type when kept in mixed cultures, but if food and water are scarce the vestigials become more viable. Rather similar but more elaborate experiments were carried out by Timofeeff-Ressovsky<sup>2</sup> who cultured samples of 150 eggs of a standard *Drosophila melanogaster* together with a similar number of eggs of various geographical races of *Drosophila funebris* under conditions of overcrowding and severe competition for food. He was able to show that, under these conditions, the survival value of *Drosophila melanogaster* was decidedly higher than that of all the strains of *D. funebris*, while the survival value of the races of *D. funebris* also differed considerably among themselves. The cases given above are also examples of competition among species or among races. Perhaps a better example of adaptability to varying conditions of the habitat is that given by Dobzhansky.<sup>3</sup> Race A of *Drosophila pseudo-obscura* ranges over regions with a hot summer, but Race B prefers a more temperate climate. Correlatively Dobzhansky found that at high temperatures race A lays more eggs than Race B, but at lower temperatures Race B lays more than Race A.

Some very interesting and informative examples of the action of selection on closely related, but sharply delimited, forms of plants have been given by Turesson<sup>4</sup> in Sweden, Turrill<sup>5</sup> and his colleagues and Gregor in England, and Clausen,<sup>6</sup> Keck and Hiesey in America and other botanists. It has been known for a long time that well marked forms of species often grow in, and perhaps are sometimes confined to, certain types of distinct habitat. Turesson transplanted several forms of this kind to his garden and found that under common cultural conditions most of them bred more or less true for their special diagnostic character. He called such forms *ecotypes*. It is considered that, over a large area, a species may possess several ecotypes enabling it to adapt itself to varying environmental conditions. With a change in the conditions of the habitat, selection weeds out those forms which are unable to react

<sup>1</sup> 1932.

<sup>2</sup> 1933 and 1935.

<sup>3</sup> 1935.

<sup>4</sup> Turesson, 1922, 1925, 1926, 1929, 1930, 1931.

<sup>5</sup> Turrill, 1938, 1938b; Marsden-Jones and Turrill, 1930-38; ditto, 1928-1938; Gregor, 1930, 1931, 1938, 1939; Gregor, Davey and Lang, 1936.

<sup>6</sup> Clausen, Keck, and Hiesey, 1938, 1940.

favourably. In this way a changed habitat may lead to a change in the frequencies of occurrence of forms of a species, thus altering the composition of the population.

The kind of investigation mentioned above is essentially experimental, for the wild species are transplanted to experimental gardens and grown together, or under different conditions for several generations. They are often called transplant experiments. As the method of experiment involves study of the plants at all stages of growth, it furnishes information about the life of plants which is otherwise unobtainable. The transplant experiments of the English school were initiated by Marsden-Jones and Turrill. We may quote a short passage from Turrill<sup>1</sup> which sums up some of their results. Over a period of ten years it was found, says Turrill, "that every species reacts differently from every other, though a classification of reactions is possible if any class is diagnosed by a certain range of behaviour. Thus, to take a few examples, *Centaurea nemoralis* survives well on all soils but shows little morphological change on any; *Plantago major* L. very quickly reacts to the different soils by most conspicuous changes in size, number, orientation, etc., of vegetative and reproductive organs: *Phleum nodosum* and *P. pratense* show, on the five soils, slowly marked quantitative differences, but these are more slowly cumulative; several species show differential death rates, with or without structural changes. The greatest and most rapid changes have been recorded for *Plantago major* L., an extremely plastic species. Here, phenotypes have been produced within two years, from seedlings and from ramets of a single clone, which have been classed as varieties and subspecies in a recent monograph of the genus. On the other hand, with two pairs of congeners, *Silene Cucubalus* Wibel (*S. vulgaris* Garcke) and *S. maritima* With. and *Phleum nodosum* L. and *P. pratense* L. there has been no approximation, on any soil, of one species to the diagnostic character of the other."

(β) *Protective Resemblance and Warning Coloration; Mimicry*<sup>2</sup>

The heading "Protective Resemblance and Warning Coloration" explains itself. It is well known that many animals attempt to conceal themselves, advertise their presence, or disguise themselves

<sup>1</sup> In the *New Systematics*, ed. by J. Huxley, 1940, p. 57.

<sup>2</sup> For "the last word on the subject" (J. S. Huxley, Introduction to Cott, 1940, page LX) consult Hugh B. Cott's *Adaptive Coloration in Animals* (1940). We are indebted to this book for much of our information.

from the possible attacks of natural enemies or predators. As Cott<sup>1</sup> puts it, "innumerable animals, inhabiting all kinds of surroundings, tend to wear on their bodies a cryptic dress." Many animals are enabled to conceal themselves from predators by the diverse colour patterns of their skins, or by shading devices which render their outlines indistinct, and make them appear to be a part of their background. Other animals seem, as it were, to advertise their presence by developing conspicuous colours such as red, black, yellow or orange. Predators learn to avoid some of these animals, for many of them are unpalatable or secrete poison, or possess a powerfully disagreeable odour, and so on.

Again, other animals appear to protect themselves from predators by means of disguise. Some, for example, resemble leaves or sticks so clearly that they can only be recognised with difficulty; others copy the outward appearance of some animal which is already protected by possession of some unpleasant feature which predators avoid. Animals which protect themselves by copying the outward appearance of other animals, or of objects, are called mimics. In Batesian mimics an unprotected species, which is usually scarce, copies a protected one, which is usually abundant. In Mullerian mimics a number of different species possessing some protective characters all look alike. The Batesian mimics may be said to deceive the predators, whereas the Mullerian mimics warn them. A phenomenon analogous to mimicry has been described in some plants, and Berg<sup>2</sup> gives several examples.

We shall now give some illustrations of the direct experimental work which has been done to show that there is a differential death rate between protected and unprotected forms of animals.

There is abundant evidence to show that various types of carnivorous animals, such as mammals, birds, lizards, snakes, fishes, etc., do not eat indiscriminately, but choose certain types and avoid other types of food.<sup>3</sup> An important and conclusive experiment on the effectiveness of concealing coloration has been performed by F. B. Sumner.<sup>4</sup> He was particularly concerned with the phenomenon of adaptive colour change of the mosquito fish, *Gambusia petruelis*, which, like many fishes, has the power of changing its colour to match its background or environment.

<sup>1</sup> 1940, p. 5.

<sup>2</sup> 1926, Chapter 8.

<sup>3</sup> See Cott, Chapter 9, for an account and general references.

<sup>4</sup> 1934, 1935, and 1935b.

Sumner first prepared the fishes for the experiments which he had planned by placing some of them in tanks painted white internally and others in tanks painted black internally for a period ranging from five to eight weeks. He found that those in the light coloured tanks became grey in colour, while those in the black tanks became black. In the actual experiments two large tanks were used, one was painted black inside, and the other pale grey. Two lots of prepared fishes in equal numbers were put into these tanks and they were next exposed to the action of the predator chosen for the experiment. Sumner used two birds for his experiments; these were the Galapagos penguin, which catches its prey under water, and a night heron, which stands in the water and seizes its prey when it comes within visual range. In the experiments with the heron the depth of water in the tank was reduced to 2 or 3 inches, while in the experiments with the penguin the depth of water varied from 2 to  $2\frac{1}{2}$  feet. Sumner found that in the pale coloured tank the penguin ate 61% black fishes compared with 39% white ones. In the black tank, however, the penguin only ate 26% black fishes compared with 74% white ones. The results of the experiment in which the night heron was used were similar to these results, but they were not quite so decisive. Using the night heron in the pale tank, Sumner reported 37% white fishes eaten as against 63% black ones, and in the black tank 60% white fishes compared with 40% black ones. The number of fishes used was large enough to give statistically significant results. The percentages of fish given above show a wide difference in the proportion of the dark and light coloured fishes eaten in the two tanks. Sumner<sup>1</sup> concludes: "*Thus for both the penguins (divers) and the heron (a wader), we have conclusive statistical evidence for the predominant selection by the birds of those fishes which were least in harmony with their backgrounds*".

An interesting and significant experiment was carried out by di Cesnola<sup>2</sup> using *Mantis religiosa*. The green form of this insect is always found on green grass, while the brown form occurs on sun-burnt grass. Cesnola collected 45 green and 65 brown specimens and tied them by means of silk threads to individual plants in the following ways:—

- a. 20 green insects were tied to green plants covered with green herbage,

<sup>1</sup> 1935.

<sup>2</sup> 1904.

- b. 25 green insects were tied to brown plants covered with burnt brown herbage,
- c. 20 brown insects were tied to brown plants on a brown patch of ground,
- d. 45 brown insects were tied to green plants on a green patch of ground.

After 18 days it was found that the protected insects (i.e., classes *a* and *c*) had all survived, while of the 25 green insects on a brown background (i.e., class *b*) *all* had been killed after 11 days exposure (20 of them by birds and 5 by ants), and of the 45 brown insects on a green background (i.e., class *d*) ten were left after 18 days and then a wind blew the remainder away. The results obtained by Cesnola are clearly in accord with the view that protective coloration has a selective effect on *Mantis*; although admittedly the number of insects used in the experiment was rather too small for statistical significance to be attached.

Very similar experiments were carried out by Beljajeff<sup>1</sup> using green, brown and yellow forms of *Mantis religiosa* on a brown background. Again, the results showed a definite selective elimination of those forms of the insects that were unprotected, i.e., whose colour contrasted with that of the background.

Carrick<sup>2</sup> performed experiments showing the predatory action of wild birds on protected and unprotected insects. He exposed various insects on various natural backgrounds near to nests of wrens, whitethroats, sedge-warblers and willow-warblers. Using their sight, these birds capture the insects, and Carrick found that they failed to notice protected insects even when perched among them. He also noticed that movements of the insects gave away their position immediately. Young<sup>3</sup> conducted a series of experiments in which various birds were given a choice of various animals as food; and he showed that protective coloration exerts a selective effect providing the animals concerned keep perfectly still. Again, the normal caterpillars and pupæ of the butterfly *Colias philodice*, are green-grass in colour, but in the course of experiments in which severe inbreeding was practised, Gerould<sup>4</sup> obtained a strain which was blue-green and behaved as a Mendelian recessive to the normal blue colour. On the normal food plant,

<sup>1</sup> 1927.

<sup>2</sup> 1936.

<sup>3</sup> 1916.

<sup>4</sup> 1921.

clover, the green insect is very inconspicuous. Gerould divided a brood of the insect into three lots: two of these were covered in, and among them a third to a quarter of the caterpillars were blue-green in colour. The third lot was left exposed to the predatory action of birds, chiefly English sparrows, and after 12 days only two tiny blue-green larvæ were found, the remainder were all green. Gerould<sup>1</sup> concluded that "it was perfectly evident that the birds had found the blue-green mutants an easy mark and that, while leaving plenty of green caterpillars untouched, they had eliminated from that part of the culture nearly every blue-green individual".

An elaborate series of experiments were carried out by Isely<sup>2</sup> in an experimental garden divided up into 96 small areas representing four types of natural background, namely black soil, white soil, red soil, and green vegetation. On these plants he placed white, black, reddish-brown and green species of grasshoppers (*Acridians*) in equal numbers in such a way that, due to their colour, they either did or did not harmonise with the background. Thus the insects were either "protected" or "unprotected" from the predators used in the experiment, which were bantams, wild birds (mocking birds, cardinal sparrow, blue jay) and turkeys. The insects were either tethered to the ground or anæsthetized. In all cases when the predators were allowed to prey separately on the insects Isely found that the percentage of eaten unprotected insects was double the percentage of the eaten protected ones. For example, when the results obtained for each predator were added together Isely reported that among the protected insects 41% were eaten and 59% survived but among the unprotected ones 86% were eaten while only 14% survived. These experiments thus provide strong evidence of the selective value of cryptic coloration in these insects although the colour variations are not inherited.

Isely also obtained evidence of the value of warning coloration in a gaily coloured conspicuous but unpalatable grasshopper (*Dactylotum pictum*). When this insect was placed on the various experimental plots the bantams and the turkey at first seized specimens but quickly dropped them, and even wiped their bills. They never made the mistake a second time.

Let us consider the application of such adaptational phenomena as protective resemblance, etc., to evolutionary problems.

<sup>1</sup> 1921, p. 403.

<sup>2</sup> 1936.



On *a priori* grounds the completely formed mimic or animal with adaptive coloration, etc., would, under certain conditions, possess an advantage over a less fortunate type. According to Darwinian ideas the former type would be naturally selected. If this is so, the protected animals should have a higher survival value than the unprotected ones. Fortunately, as we have seen, this contention has been examined experimentally. In point of fact, the theories of protective resemblance and so on are looked upon as very important bulwarks of the general theory of natural selection. Cott<sup>1</sup> remarks: "When the theories of Protective Resemblance, Warning Coloration and Batesian and Mullerian Mimicry were first propounded, they were open to one very serious objection, namely, lack of evidence that the schemes of coloration actually serve the functions assigned to them. This criticism is no longer admissible. The last fifty years have seen an immense number of observations in the field and the application of experimental methods to test the validity of these theories." And again: "The evidence available today is no less clear in regard to warning coloration. Such evidence, direct and indirect, whether derived from comparative studies of natural groups or from feeding experiments, from the observed behaviour of wild animals or from the records supplied by the food in their stomachs, indicates that different insectivorous and carnivorous predators discriminate in the choice of food; that they quickly learn to recognise and to avoid unpalatable prey; and that aposematic animals do in fact enjoy considerable immunity from attack."<sup>2</sup>

The examples of protective coloration and the like given seem very convincing, but whether or not they show that a beneficial adaptation in a truly wild state has any positive evolutionary value is another matter. Our senses tell us that it is easier to see a white butterfly against a black background than a black one on the same background, but in a natural state extremes of colour in background are rarely met with over a wide area. In fact, the natural background is on the whole kaleidoscopic in colour and animals move from place to place. Again, it has been shown that the really important feature about mimics and protectively coloured animals is that they remain inconspicuous only as long as they keep still. As soon as they make even a slight movement the predator sees and seizes them. On the other hand, even in animals which are

<sup>1</sup> 1940, p. 435.

<sup>2</sup> *ibid.*

commonly thought to be protected due to their colour, dimorphic forms may exist. A handy summary of such forms has been given by Elton,<sup>1</sup> an ecologist. The simplest example is that of the white arctic fox, which, as it lives among snow, would seem to be perfectly adapted to its surroundings. According to current Darwinian views this species of fox has been evolved by natural selection of those animals which possessed lighter coloured fur. In actual fact, as Elton points out, the arctic fox exists in two colour phases, one white in winter and brown in summer, and the other blue in winter and grey or black in summer. In many parts of the arctic regions the blue and white phases occur indiscriminately in a common population. Selectionists have then to face the question that if the one of these colours which is adaptive evolved by means of natural selection, how did the non-adaptive one evolve at the same time and in the same place, or why hasn't it long since been exterminated by selection? There are many other cases of this kind and there are many other field naturalists who have come up against similar problems when studying animals in their natural surroundings.<sup>2</sup>

### (c) *Natural Selection and Evolution*

The few samples of the evidence for the occurrence of natural selection already given show that a cumulative argument may be advanced to the effect that under certain environmental conditions certain types of the same and of different species may be discriminated against in nature and exterminated quicker than other types. None of the examples given, however, satisfy all of Pearl's requirements (p. 321) of a proof that a race has been altered by selection. It is one thing to show that natural selection does actually operate, and another to show that it plays a part in changing one species into another; that is, that selection is a causal agent in bringing about the evolution of species.

The scientific work of selectionists indicates that natural selection

<sup>1</sup> 1927, Chapter 12.

<sup>2</sup> For further information on this interesting subject the reader is referred again to Cott (1940). The views of eminent authorities both for and against the theories of mimicry and protective coloration are given in a series of letters in *Nature* (1936, H. E. Armstrong, p. 242; G. D. Hale Carpenter, pp. 243, 686-687; E. W. MacBride, pp. 365-366, 884-885; J. B. S. Haldane, p. 1053; and E. B. Ford, pp. 1053-1054). Criticisms are also given by McAtee (1932) and Heikertinger (1933-36).

is a causal agent in evolution, and so they use this perfectly legitimate hypothesis to help them to interpret the phenomena of evolution. Robson and Richards,<sup>1</sup> however, have pointed out that if natural selection acts as an important factor in evolution, we should expect to find that those features which distinguish closely allied species and varieties would very frequently show obvious and clear cut adaptations with definite survival value. It is, however, well known that very many species or varieties differ only slightly from each other and that the characters separating them have no obvious adaptive value. To suggest that the slight non-adaptive varietal or species character concerned is linked with a character which is adaptive but unknown may point the way to further investigation, but, as far as we know, no one has travelled along it.

If it be granted that natural selection exerts a choice on certain favourable types, then it is reasonable to assert that it also gives an efficient explanation of the perpetuation (but not the origin) of certain adaptations and by doing so it may then exert a powerful influence on the trend of the evolution of species, but it does not necessarily determine the course of evolution. The association of natural selection with evolution in this way creates a difficulty, as Diver<sup>2</sup> has so ably pointed out, for natural selection, while working to limit adaptation, in the sense that it is a conservative agent, must at the same time be involved to explain the very great variety and general nature of the adaptability of all species. Diver also points out that for this to be possible a high mutation rate is necessary in successful species. It would seem that without frequent mutations of a cumulative kind on which selection can work, it will tend to keep a species stable. Given advantageous, frequent and cumulative mutations, selection would seem to exert a directive influence on evolution. There is, however, no positive evolution showing that a gene mutates continuously in one direction only for any very long period of time. Occasionally a gene alteration produces a phenotypic change of relatively great magnitude, and, given certain conditions, selection has been known to produce an observable change of appearance in a local population, as in the case of Heslop Harrison's melanic forms of *Oporabia autumnata*. In such cases a new variety survives, but it need not (and indeed does not) supplant the original type. Selection in such cases is aiding the divergence of species.

<sup>1</sup> 1926.

<sup>2</sup> 1936, p. 63.

While in the absence of frequent mutations, the day by day action of natural selection on species may be a stabilizing one running counter to any evolutionary change it may equally as well stabilise beneficial mutations and thus play a part in what may be called microevolution. J. R. Baily<sup>1</sup> finds that physiological variations in organisms are often more pronounced than morphological ones. Examples of variation of this type are seen in the physiological races of many fungi, particularly the rust and smut diseases of cereals, the physiological varieties of snails and in *Drosophila pseudo-obscura* which has two morphologically indistinguishable geographic races. These, however, differ in the duration of the developmental stages and rates of oviposition,<sup>2</sup> and in their physiological reactions.<sup>3</sup> Baily considers that there is an increasing amount of evidence to show that natural selection may act by eliminating those individuals which are physiological misfits.

We have attempted in this and preceding chapters to give the reader some general impressions of the past and present ideas of the rôle and value of natural selection in organic evolution. When all is said and done and whether or not one assigns to natural selection a major or a minor rôle in evolution, it is clear that since the popularization of the idea of natural selection by Charles Darwin, biology has advanced very rapidly indeed, at a rate many times greater than could have been predicted from the state of the science in 1859-60. Undoubtedly the reason for this advance is that the application of selection to evolutionary problems has enabled biologists to solve many outstanding problems and helped them to commence a synthesis of biological ideas. The subject of biology is taking its place as an exact science, young, vigorous and fresh, no doubt, but still no longer in the dark and uncertain embryonic stage. The birth pangs of biology as an emerging science are past; the teething troubles have yet to come. The concept of evolution is a vast one, like the concept of eternity, and just as this concept enables us to grasp and explain some eternal phenomena, so on a lesser plane does natural selection enable us to understand some of the phenomena of evolution. The justification of the selection theory lies in the fact that the multififormity of evolution finds a logical and formal *argumentum ad iusticiam* in the universality of selection in the organic world.

<sup>1</sup> 1941.

<sup>2</sup> Shapiro, 1932.

<sup>3</sup> Dobzhansky, 9351.

## EPILOGUE

“ Evolution is a philosophical conception ” (Dewar)

“ Evolution is a philosophy ” (Hogben)

“ Evolution is an incontrovertible fact ” (J. S. Huxley)

HOGBEN<sup>1</sup> has enunciated four principles which he considers led to the formulation of the modern theory of evolution. These are (a) the principle of biogenesis, which considers that existing organisms arise only from existing organisms, (b) the principle of unity of type which followed from the study of classification and comparative anatomy, (c) the principle of succession as shown by the fossil record, and (d) the principle of genetic variation uncovered by genetic studies. These principles were discovered in the order given and they have been dealt with in the chapters on the Speculative Period, Period of Formulation and the Modern or Synthetic Period. The modern evolution theory, however, is only a part of a larger idea, the idea of change, which has its roots in the philosophical notions of antiquity. This side of the development of evolutionary doctrine has been covered by the sections in Chapter I on the Obscure Period and the Greek and Mediæval Period. We have presented enough evidence to show that the philosophical idea of change supplies the *raison d'être* of the evolution idea. This philosophical notion of change has always been widely held and it is probably true to say that the strength of the appeal of the modern theory of evolution lies in the fact that the observational and experimental data discovered by empirical science, which led to a conception of organic evolution, fitted neatly into a niche already prepared for them by the philosophers. It follows that “ Evolution is a philosophical conception ” as Dewar<sup>2</sup> says. Hogben goes even further and considers that evolutionary doctrine forms an “ interpretative hypothesis ”. The need for such a hypothesis springs from an intellectual curiosity which, if satisfied, provides us with a philosophical system. Hogben concludes that “ Evolution is a philosophy.”<sup>3</sup>

<sup>1</sup> 1930, p. 193.

<sup>2</sup> 1931, p. 1.

<sup>3</sup> 1930, pp. 146-150.

In our historical account of the evolutionary concept we have not attempted to give any *formal* presentation of what is called the classical evidence for the occurrence of organic evolution. This is to be found in any textbook of evolution under the headings of (a) evidence from comparative anatomy, (b) evidence from the geological succession, (c) evidence from geographical distribution, (d) evidence from classification, (e) evidence from embryology, (f) evidence from serology, and (g) evidence from genetics. The first five lines of enquiry were known to Darwin, and he was, in fact, the first naturalist to bring together the various facts and findings from these diverse branches of natural history, and to present them as evidence of a cumulative kind for the occurrence of organic evolution. As necessity required, this evidence has been mentioned in the various sections of this book in an endeavour to show how the idea of evolution developed in the minds of naturalists. The evidence from each branch of natural history mentioned above is suggestive only, and by a cumulative argument it is found that the facts of the case fit into a rational scheme if interpreted in an evolutionary sense.

The classical evidence for the occurrence of evolution is, then, indirect and circumstantial and furnishes us with a theory of evolution. Acceptance of this theory enables biologists to unify their science into one grand scheme which helps them to interpret other facts and occurrences in the natural world, which, before acceptance of the theory, remained aloof and which often seemed to be self-contradictory. The justification for the theory has been shown to be its workability.

Biologically, a belief in the theory of organic evolution in its strictest and purest form entails also a belief that all organisms living and dead are ultimately descended from, or traceable back to, an extremely simple and primitive type of living thing which itself sprang from, or arose out of, inanimate matter. The idea of spontaneous generation is as old as the idea of change but it has never been actually observed. It is sometimes said that organic evolution is not concerned with the ultimate origin of living things. The evolutionist must take living things as he finds them, or can discern what they were like in past ages from the records of the rocks. He starts with life and attempts to trace out the way and the methods by which organisms have changed. If, however, an evolutionist holds to a general cosmological evolution, in which is visualised a general change of matter from a relatively simple mass to a complex

state of integrated wholes, then he must also take into account the question of the origin of life. In cosmological evolution we can imagine change taking place starting from electrons, to atoms, simple molecules, complex chain molecules, ultramicroscopical particles, unicellular organisms, and finally to multicellular organisms. In this series the origin of living things is merely a transitional stage within the general scheme.

As the idea of evolution concerns changes from simple to more complex things, the simplest original living thing would be that first mass of matter which, by its own powers, was capable of growth, development and reproduction. Viruses present a problem to those who seek to give a comprehensive definition of "life". They produce definite effects on organisms and seem to be able to reproduce themselves, although they do not show signs of the usual life processes such as assimilation and metabolism. When separated from the plant on which they are growing they seem to be only crystallizable proteins, but they have never been known to function in the absence of living protoplasm. Some people regard them as living things, others dispute this and regard them more as products of living things, and others again look upon them as things which are on the way to becoming organisms. At present, however, the viruses do not furnish a suitable starting point for any accepted scheme of evolution. Again, the oldest known fossils, such as the trilobites, do not help the evolutionist in his search for a starting point, for they are already too complicated in structure. Theoretically, then, the evolutionist is forced to postulate a mass of primitive protoplasm with all the powers of protoplasm as the starting point of living things. As to the origin of such primitive protoplasm he can at present only speculate about the matter, unless indeed he admitted its special creation whole and intact. This the evolutionist, so long as he remains bound by his scientific ideas and for the sake of his scientific methodology, will not do, and indeed cannot logically do, for the aim of natural science is to interpret natural events in terms of natural causes.<sup>1</sup> By the very nature of things no one can know with absolute certainty how living things arose in past ages, and in actual fact, although there is a host of speculations, there is no truly scientific evidence to show how this process took place.

The evidence for the truth of the evolution idea is truly scientific

<sup>1</sup> To accept this statement does not imply that the doctrine of derivative special creation cannot be held too.

and experience has shown that its use in biology provides a rational explanation of many of the outstanding problems raised by the mere *existence* of species or of individuals. As a famous biologist<sup>1</sup> has written: "The nature of the proof of organic evolution, then, is this: that, using concept of organic evolution as a working hypothesis, it has been possible to rationalise and render intelligible a vast array of observed phenomena the real facts upon which evolution rests. Thus, classification (taxonomy), comparative anatomy, genetics, become consistent and orderly sciences when based upon evolutionary foundations, and when viewed in any other way they are thrust into the utmost confusion. There is no generalisation known to man which is of the least value in giving these bodies of fact any sort of coherence and unity. In other words, the working hypothesis works, and is therefore acceptable as truth until overthrown by a more workable hypothesis." That the theory of evolution has solved only a relatively small number of biological problems concerned with the origin of things is unfortunate, but this fact does not vitiate the cogency of the arguments in favour of an evolution of species.

As there are no philosophical or theological objections to the idea of change itself, reputable philosophers and theologians do not necessarily see anything repugnant in the scientific theory of evolution. Two questions from men widely different in outlook and training from H. H. Newman quoted above will serve to emphasize this fact. First we may quote Messenger,<sup>2</sup> who writes: "As to the *evolution of species* we consider that the *scientific* evidence, consisting as it does of so many converging lines, is sufficient to give a fairly high degree of certitude concerning the *fact* of, at any rate, *some* evolution, though opinions must necessarily differ as to the *mode*. And from the *theological* point of view, we consider that evolution is the only reasonable way of harmonizing our modern knowledge of the succession of geological epochs, with their flora and fauna, with the scriptural statement that the earth produced all the present-day species." Mgr. Janssens<sup>3</sup> writes: "Further, the opinion admitting the passage from one order to another, for instance from the vegetable order to the animal order, is not basically opposed to the scholastic principle according to which forms are not generated by other forms, but are brought forth from

<sup>1</sup> H. H. Newman, 1935, p. 51.

<sup>2</sup> 1931, p. 274.

<sup>3</sup> In *De Deo Creante*, quoted and translated by Messenger, 1931, p. 81.



the potency of matter. Hence the scholastics themselves admitted a certain spontaneous generation. And once this is allowed for the inferior animals, there does not seem to be a very stringent reason for confining the power of transformation to these alone."

A biologist, as a biologist, is not unduly worried about the fact of evolution. It is a completely different matter, however, when, following the fashion of the times, he projects his biological ideas into his philosophical life. Every man is a philosopher, and so it is probably a good thing that natural happenings should make a man stop and think about the nature of things in general. It is in fact his right to do so. The danger, however, is that some scientists stop short at the very point at which their truly philosophic reasonings should begin, with the result that their philosophy is made to fit in with their biological theories, instead of interpreting their theories on the basis of principles founded on practically innate and probably surer mental convictions. Our historical account has attempted to show that this was the great fault of many of the Darwinians and led to much bitterness and heart searchings. It was particularly unfortunate that Darwin's great book was published during what may be called the golden age of materialism. The theory of evolution which developed at this time and which was really in essence a theory of evolutionary adaptations, was necessarily mechanistic. The Darwinian conceptions, however, while they indicated that evolution was brought about by the operation of natural causes, also seemed to indicate that these causes act fortuitously. The only guiding factor in the process seemed to be that of a progression towards greater complexity in organisms as they evolved, a passage from homogeneity to heterogeneity. And so the Darwinian evolutionary ideas became coupled to the philosophic idea of progress and to materialistic philosophy so prevalent at the time. This philosophy, however, has severe limitations; by the exclusion of teleology it excludes finality and thereby limits the extent of its own generalizations. So a theory of evolution (or of evolutionary adaptations) which was bound up with such a philosophy also became limited in the scope of the interpretations which it could give to natural organic happenings. Interpretations, then, founded on Darwinian ideas developed on such lines, take us far along the path of understanding of organic evolution but do not enable us to comprehend the process to any greater extent than a theory founded on a teleological basis.

It would be wrong to conclude without referring to those

biologists and others who do not believe that evolution is a fact in any but an extremely limited sense. As already stated this book is an account of the history of the idea of evolution, and not an account of the arguments for or against the validity of the concept. Excluding purely biological reasons, we believe that the concept is a valid one because the idea of change on which it is founded has been, and is, so universally held.

There are others, however, who do not subscribe to the theory of evolution because they consider the known facts, although capable of a partial explanation by means of the evolutionary theory, cannot be completely so explained and are more convincingly interpreted by a modified form of special creationism which allows for the operation of some evolution. The reader will find these points discussed in Douglas Dewar's *Difficulties of the Evolution Theory* (1931), and *More Difficulties of the Evolution Theory* (1938). In these books, and in other writings, Dewar attacks the theory from various possible angles, but chiefly on palæontological grounds, and he deals in detail with various difficulties encountered by biologists which, he contends, are irreconcilable with the theory of evolution.<sup>1</sup>

Let me conclude by summarising the history of the idea of organic evolution. The conception of organic evolution had its basis in a philosophical notion of change involved in the idea of "coming-to-be" and "passing-away". In the early and great systems of philosophy, such as that of Aristotle, the pre-eminent features of the external world which forced themselves on the minds of the philosophers were those of motion and change. In the Aristotelian system the intelligible explanation of these features led to the development of a theory of matter and form, i.e., it led to a recognition of material and non-material worlds which were considered to be inter-related. During this time, which persisted through the scholastic period up to about the time of the Renaissance, natural historians and philosophers seemed to be looking for

<sup>1</sup> In 1941 the author became involved with Douglas Dewar in a lengthy controversy on the merits and demerits of the theory of evolution (see Bibliography under Dewar, O'Gorman, Polimeni, and Fothergill). In the course of his discussions, Dewar mentioned the most important of those biologists who either completely disagree with the idea of evolution or who doubt its general applicability. For readers who are interested I give most of these names below; references to their writings will be found in the Bibliography: L. Vialleton (1929), G. B. O'Toole (1933), A. Fleischmann (1901, 1933), L. Merson Davies (1935), Heribert Nilsson (1935, 1939), E. L. Grant Watson (1938), P. Lemoine (1928), J. Lefevre (1938), E. Guyenot (1930), Rendle Short (1935), and W. Morley (1939).

such a conception as that of organic evolution. But while they held to a philosophical idea of change they also believed in the immutability of species. During the Renaissance new ideas developed and empirical science advanced and the idea of change became crystallized in the thoughts of naturalists, and, like crystals, it came to possess clear-cut edges, which imposed a limit on its further expansion. In this period the naturalist attacked organic evolutionary problems by working backwards in attempting to classify organisms into schemes of relationship. From these schemes, however, sprung the realization that species were changeable. No matter how we define species, philosophical enquiry reveals that there is no objection to the idea of their mutability. Once this point was established the idea of change in the organic world gave birth to a definite theory of evolution in the modern sense. The curiosity of naturalists was roused and it was satisfied by probing, at first speculatively and later experimentally, into the methods or causes of evolution.

It was during this period that Lamarck published his essentially teleological views and thereby began a controversy about the methods of evolution which extends up to the present day. Next came Charles Darwin, whose apparently anti-teleological ideas gripped the imagination of the biological world so strongly. The next decisive step in the history of the idea of evolution was taken by de Vries who rediscovered the work of Mendel and produced his own extensions of the comparatively new theory of heterogenesis or mutations, while at about the same time Bateson, Morgan and many others began those experimental investigations which led to the extension of Mendel's basic principles into the formal science of genetics.

During this period the ideas of these various investigators on the nature of the changes in species, like many other new ideas, at first seemed to be mutually antagonistic. The contemporary multiplicity of the causal theories of evolution seemed only to complicate the issue and naturally enough led to some confusion. In the last decade or two this confusion has been dispelled to some extent by those workers like Muller, who first induced mutations, and to those like Timofeeff-Ressovsky who showed that in nature wild populations of organisms are often full of small heritable mutations similar to the experimental ones known and induced in the laboratory, and also to those like Goldschmidt, whose work seems to show that the essential unity of organisms does not imply the

operation of only one process in evolution. An important point which emerges from the modern work on evolutionary problems seems to be that unity in the organic world is obtained by the conservative beneficence of a rule of law, not by the operation of a rule of chance. The modern synthesis of evolutionary theory fully recognises the Darwinian position which changed the earlier teleological ideas of change into a materialistic form. The modern view may be mechanistic (as it is concerned with empirical science it must be) but there is little reason why it should now be coupled with a purely materialistic philosophy. For purposes of study, scientism, including evolutionism, may ignore teleology without denying it, but it does not follow that teleology must be excluded from any generalization which is arrived at by means of this method of study, for, before these generalizations can become regarded as fundamental in a wider philosophic sense, they must take in the whole of knowledge which includes the possibility that teleological causes exist in happenings of which scientism describes only a part.

Finally, there is a certain amount of direct evidence for the occurrence of evolution. A number of biologists have succeeded in producing "new species" by direct experimental methods, and others have produced evidence demonstrating how new species may have actually arisen in nature. Most of these cases have been mentioned in the text already. Whether or not we agree that the individuals produced experimentally are new species does not matter. What does matter is that they are entirely new and unpredictable organisms which have arisen from pre-existing organisms and are sufficiently different from the original parents to justify biologists in calling them new species. They are, at any rate, *new forms*. Hence J. S. Huxley<sup>1</sup> may well write, "Evolution is an incontrovertible fact", for he does not really mean by this statement that evolution is an absolute fact, but that evolution is true as far as our present knowledge goes. The scientist always makes that mental reservation whether or not he takes the trouble to point it out to his readers. The scholastic philosopher Maritain<sup>2</sup> writes: "The truth of knowledge consists in the conformity of the mind with the thing. It is absurd to doubt the reliability of our organs of knowledge." Very many working biologists, and also others who perhaps have a wider but less specialised knowledge, will accept that statement at its face value, for they know by experience that the

<sup>1</sup> Chapter headlines in *The Science of Life*, Vol. 1, Book 3.

<sup>2</sup> 1946, p. 136.

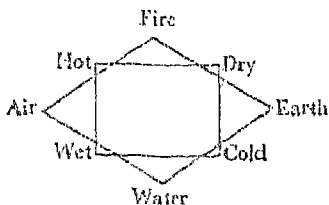
progress of biological knowledge depends on its acceptance whether qualified or not.

The experimental research that flowed from the basic ideas of Mendel has thus been fruitful in the stimulation which it gave to the development of evolutionary ideas for it has brought out vividly the relation between empirical and mathematical interpretations of biological events on the one hand, and a process in the organic world which is historical by definition and philosophical by implication on the other hand. It is probably safest and wisest at the present time to conclude that whereas experimental methods in evolutionary biology offer much hope for the future, at present they can only investigate small-scale aspects of evolutionary differences between existing organisms. At present such methods seem to be limited in their applicability to the historical side of evolution, for, in spite of intensive research, they can neither take us back into the past, nor project us into the future.

## APPENDIX I

### ARISTOTLE'S THEORY OF MATTER AND FORM

Natural things are either substances, or functions and attributes of substances. Aristotle classes bodies, which may be either simple or composite, as substances; while by their functions or attributes he means their movements and alterations.<sup>1</sup> All philosophies previous to Aristotle's considered that natural composite substances were due to the "coming-to-be", or "passing-away", of the primary elements. Aristotle held to this view and followed Empedocles by distinguishing primary elements, namely earth, air, fire and water. These elements, however, have no separate existence, they are always connected with, or in association with, their corresponding contrariety.<sup>2</sup> Hence, from the four elements are derived their four qualities, hot, cold, wet and dry. A quality is not a substance, but a substance always has some quality—the same substance may even be the basis of several qualities. For instance, a cold body may be wet, or cold, or hot, etc., in turn. Hence Aristotle postulates an underlying matter which he calls potentially perceptible body: "We therefore have to recognise three 'originative sources': firstly, that which is potentially perceptible body, secondly, the contraries (I mean, e.g., heat and cold), and thirdly fire, water and the like."<sup>3</sup> Aristotle expands these ideas in detail throughout the rest of book two of *De Generatione et Corruptione*. He<sup>4</sup> points out that the four primary elements can be combined in six ways of two each, but contraries cannot be so coupled, for example, a thing cannot both be hot and cold, or wet and dry, at the same time; it can be hot and dry however. Hence the primary qualities can only be combined in four different ways. The relationship between the elements and their qualities is expressed as follows:—<sup>5</sup>



Thus to Aristotle matter was made up of these four primary elements,<sup>6</sup> and each of these was made up of two primary qualities. All matter is thus composed, and here there is no distinction between animate and inanimate things. Hence the definition of matter is given as "the primary substratum of each thing from which it comes to be without qualification, and which persists in the result."<sup>7</sup> The common opinion is that "coming-to-be" means a change into perceptible

<sup>1</sup> *De Caelo*, 298a, 30.

<sup>2</sup> *De Gen. et Cor.*, 328b, 25.

<sup>3</sup> *ibid.*, 328b, 33.

<sup>4</sup> *ibid.*, 329b, 30.

<sup>5</sup> After Singer, 1941.

<sup>6</sup> *De Gen. et Cor.*, 334b, 31 and 335a, 9.

<sup>7</sup> *Physica*, 192a, 31.

material, while a change into invisible material indicates a "passing-away".<sup>1</sup> But, according to Aristotle, this opinion is not completely correct because a further distinction must be made, that is, a distinction between qualified and unqualified coming-to-be or passing-away. These distinctions depend upon differences in the material which changes for it can be (a) substantial, or (b) more or less substantial, or (c) more or less perceptible.<sup>2</sup>

Coming-to-be is cyclical for things thus "return upon themselves" and this conclusion harmonises with Aristotle's views about the eternity of the celestial circular motion.<sup>3</sup> He thus prevents the behaviour of celestial and terrestrial bodies from clashing, for the originative sources of both are then eternal. Some things, such as showers of rain, behave in this cyclical way, but others, such as men and animals, do not, for the same individual comes to be only once. Here it is the *species* which returns upon itself, not the perishable individual of the species.<sup>4</sup> Thus Aristotle indicates here quite definitely that, although individual animals or plants may perish, the *species*, whose exact nature is determined by the specific form, is *immutable*. This would seem to indicate also that he did not believe in evolution as we conceive of it because the mutability of species is the foundation stone of the theory of organic evolution.<sup>5</sup>

This conception of matter is concerned only with the *materia prima*, or primary matter. It is not any particular *thing*, for then it would not be primary. Hence, it is incomplete and it is not knowable by the human senses. These can only appreciate it by means of *form*. Without form matter is a real entity, though incomplete and only potential.<sup>6</sup> Substance, or what we ordinarily call matter, is not the same as this primary matter of Aristotle, because we can know ordinary substances by our senses. To him the word substance has three meanings—form, matter, and the complex of both—"and of these three what is called matter is potentiality, what is called form is actuality."<sup>7</sup> The complex of both produces what we ordinarily call matter, the secondary matter of the Thomists. The form then gives shape to things. It is form which makes a thing what it is. Thus, when we know a thing it is known as a Form which is the active principle, the primary reality, because that which is most *known* is the most real. The underlying potential basis of everything is matter which is immutable and eternal. What we usually refer to as "nature" is the form of the thing rather than the matter, because, as matter, the thing exists only potentially, whereas it is the form which gives it actuality: with actuality it can be said properly to exist.<sup>8</sup>

## APPENDIX 2

### ARISTOTLE'S CLASSIFICATION OF ANIMALS

Aristotle, following Democritus, divided animals into two distinct groups, (a) those with blood and (b) those without blood. By blood he means *red* blood (possessing oxyhæmoglobin), and this grouping corresponds almost to our vertebrate and invertebrate divisions. He could not be expected to know that some invertebrates, like *Planorbis* and others, possess red blood too but which does not

<sup>1</sup> *De Gen. et Cor.*, 318b, 20.

<sup>2</sup> *Ibid.*, 318b, 35.

<sup>3</sup> *Ibid.*, 338a, 18.

<sup>4</sup> *Ibid.*, 338b, 6-14.

<sup>5</sup> See also *De An.*, 415a, 25.

<sup>6</sup> cf. Phillips, 1934, Vol. 1, p. 4.

<sup>7</sup> *De An.*, 414a, 16, and 412a, 6.

<sup>8</sup> *Physica*, 193b, 7.

contain hæmoglobin. His genera of animals were often dealt with in an ascending or descending order, but he soon came up against a difficulty among the lowliest bloodless forms. "Sometimes it is a matter of doubt whether a given organism should be classed with plants or with animals."<sup>1</sup> In modern times we experience the same difficulty but concerning different organisms.

The sponges, for example, he seems to consider as definitely plants.<sup>2</sup> These organisms are attached to rocks, and when separated they die; they have no sex. Apparently they possess a certain sensibility but Aristotle seems to be rather dubious about this.<sup>3</sup> The *Holothuroidea* (sea cucumbers, sea-lungs) are a little different from the sponges (actually they are echinoderms) in that they live unattached to any rock. Their life, nevertheless, is "simply that of a plant separated from the ground".

Some of the *Testacea*, or *Ostracoderma*, resemble the *Crustacea*, while others are more like the cephalopods.<sup>4</sup> Aristotle recognises here numerous genera and species, the chief ones being—(a) the *Turbinata* or whelks, (b) the univalves, (c) the bivalves and (d) the sea-urchins and ascidians. These latter present difficulties, and seem to be intermediate between plants and animals. They have, however, more of an animal nature than sponges for their body is flesh-like, and they seem to be slightly sensitive to touch. But, on the other hand, like plants, they excrete nothing and they are always attached to rocks, or substratum of some kind.<sup>5</sup> The testaceans as a whole also seem to be intermediate between plants and animals. "As plants they have no sexes and one does not generate in another; as animals they do not bear fruit from themselves like plants, but they are formed and generated from a liquid and earthly concretion."<sup>6</sup> With the exception of the sea-urchin (which has no soft parts), all of the testaceans possess some kind of external shell and an inner soft fleshy part. In the ascidians all of the soft part is enclosed by the hard part. In the following group of *Acalephæ* (sea-anemones, sea-nettles), which are really coelenterates, all of the body is soft, none is hard. According to Aristotle the soft part of a sea-anemone corresponds to the soft part of an oyster, while the shell of the latter is represented in the anemone by the stone on to which it is fastened.<sup>7</sup> These sea-nettles are not testaceans but, like them, they seem to be intermediate between plants and animals. Some are attached to rock, like plants, and these void no visible excrement. Others of them can detach themselves; these are sensitive to touch, and can grasp food and hence must be considered to be animals.<sup>8</sup>

Succeeding groups of animals are perhaps best dealt with according to the method of reproduction, and, in fact, Aristotle uses the various methods of reproduction for classification.<sup>9</sup> Naturally enough he finds it difficult to produce clean cut classes, there is some overlapping when the generative methods are considered in relation to the other criteria of classification. Nevertheless this way of classifying things seems to be a perfectly natural and obvious one for Aristotle to choose, for reproduction is of fundamental importance to the animal in order that it may partake in the eternal. "For since it is impossible that such a class of things as animals should be of an eternal nature, therefore, that which comes into being is eternal in the only way possible. Now it is impossible for it to be eternal as an individual (though of course the real essence of things is the

<sup>1</sup> *De Part. An.*, 681a, 15.

<sup>2</sup> *De Part. An.*, 681a, 15, and *H. A.*, 588b, 20, and 548b, 27.

<sup>3</sup> *H. A.*, 487b, 9.

<sup>4</sup> *De Part. An.*, 684b, 16.

<sup>5</sup> *De Gen. An.*, 761a, 15, and *De Part. An.*, 681a, 27.

<sup>6</sup> *De Gen. An.*, 731b, 10.

<sup>7</sup> *H. A.*, 590a, 31.

<sup>8</sup> *H. A.*, 531b, 9; 548a, 24; 531a, 31, and *De Part. An.*, 681b, 1.

<sup>9</sup> *De Gen. An.*, 732a.



individual)—were it such it would be eternal—but it is possible for it as a species.”<sup>1</sup> That is, the species is continued by generation and hence is eternal. Aristotle further refers to this topic in the *De Anima*.<sup>2</sup> The species is indeed immutable, “it continues its existence (by generation) in something like itself—not numerically but specifically one”.

In considering Aristotle's classification using these criteria we must always bear in mind the difficulties under which he worked and the things he could not possibly know. For instance, he could not know anything about the mammalian ovum; while the number of actual species he had to examine was ridiculously small for him to generalise from. The marvel is that he accomplished so much and could consider first principles in relation to generation. Aristotle did not, of course, know anything about fertilisation. We must remember that to him the female was a purely passive agent in reproduction, the male was considered to be the active moving agent. The female provides the material for the semen, which contains the form, to activate.<sup>3</sup>

It is not even necessary for anything to pass from the semen to the female in order to produce an embryo, as long as motion and form are imparted to the female material.<sup>4</sup>

We can compare this with our modern knowledge of artificial parthenogenesis in which various ova have been made to develop without fertilisation merely by artificial stimulation, such as by pricking, or by chemical means by the addition of salts to the liquid medium containing the eggs. In modern language, fertilisation is primarily a process of activation.

While Aristotle did not consciously attempt to divide up the then known animal kingdom on the basis of the way in which they produced their young, it is obvious from the *Historia Animalium* and the *De Generatione Animalium* that he had some ideas at the back of his mind that such classification could be compiled. He is continually referring to viviparous animals and comparing them with oviparous ones. Moreover, Aristotle, having considered the various ways in which animals reproduce, finds that “Nature orders generation in regular gradation”. Starting with the least perfect and coldest animals, and proceeding up to the highest or most perfect and hottest forms, we pass through various stages beginning with those animals which produce a scolex, through those with imperfect eggs, perfect eggs, to those which produce their young directly from the parents. Aristotle does not recognise this as being anything more than a regular gradation or series. He does not attempt to look for clues as to the development of sex, or the sex processes.<sup>5</sup> There is some overlapping in this scheme, but, nevertheless, Aristotle saw that the more perfect the animal the more perfect the way in which it produces its offspring.

In the *Historia Animalium*<sup>6</sup> we read: “Again, some animals are viviparous, others oviparous, others vermiparous or grub-bearing”. Examples of these are:—viviparous—man, horse, seal, etc., and the marine animals the *Cetacea* and the *Selachii* (cartilaginous fishes); oviparous—birds, tortoise, lizard, frog, etc.; vermiparous—insect. “Of viviparous animals, some hatch eggs in their own interior, as creatures of the shark kind, others engender in their interior a live foetus, as man and the horse. When the result of conception is perfected with some animals a living creature is brought forth, with others an egg is brought to light, with others a grub.” Again, “What we term an egg is a certain completed

<sup>1</sup> *De Gen. An.*, 731b, 32.

<sup>2</sup> 415b, 1.

<sup>3</sup> *De Gen. An.*, 729b, 34.

<sup>4</sup> *De Gen. An.*, 729b, 17.

<sup>5</sup> *De Gen. An.*, 733b, 1.

<sup>6</sup> 489b, 1.

<sup>7</sup> *H. A.*, 489b, 11.

result of conception out of which the animal that is to be develops, and in such a way in respect to its primitive germ, it comes from part only of the egg, while the rest serves for food as the germ develops. A grub, on the other hand, is the thing out of which the animal in its entirety develops, by differentiation and growth in the embryo."<sup>1</sup>

Bloodless animals either give an egg or produce a scolex. This is a new term which Aristotle introduces into the *De Generatione Animalium* but he does not seem to mention it in the *Historia Animalium*. It is important to understand what he means by it. The insects reproduce characteristically by producing a scolex and even if the insects are spontaneously generated they still come from a scolex. The difference between a scolex and an egg is that in the former the whole develops into a new animal, while in the latter only a part develops into a new embryo, the remaining part serves as nourishment for it. Insects then produce a scolex, which is the grub.<sup>2</sup> The scolex grows till it reaches full size and then forms a kind of egg, i.e., it becomes a pupa which Aristotle thought to be an egg because of the hard case and the resting insect inside. From this is produced a new insect. The difference between egg and scolex is thus merely one of nutriment. Platt in his footnotes to his translation of *De Generatione Animalium* reminds us of the comparison of this conception of Aristotle's and the modern distinction of eggs with holoblastic yolks, the whole of which develops into the body of the embryo, and meroblastic yolks, in which only a small part so develops, the rest being nutriment.<sup>3</sup> Both eggs and scolex grow until they reach full size. In the former it is a growth toward completion involving no change in form, but in the latter there is a change in form; the scolex, in fact, becomes a pupa. In one sense *all* animals generate by producing a kind of scolex "first since the most imperfect embryo is of such a nature; and in all animals even the viviparous and those that are by a perfect egg, the first embryo grows in size while still undifferentiated into parts; now such is the nature of the scolex".<sup>4</sup> The scolex, as we shall see later, gives us another glimpse of Aristotle's possible evolutionary ideas, here concerning the origin of man.<sup>5</sup>

Now that we have considered these various details, it remains to see in what relation Aristotle seems to view the various animals he dealt with. Except for the very lowliest forms we shall use their methods of reproduction as our chief criterion in classifying them, and we shall begin with the most imperfect forms, proceeding up to the highest, or most perfect, types ending with man. This order of perfection seems to be that indicated by Aristotle. Ogle<sup>6</sup> also used the reproductive faculties as a basis for extracting a classification from Aristotle; he also gives a full discussion on the meaning of perfection in animals. The use of the terms moist, dry, hot and cold here indicates that Aristotle interpreted the form and functions of the animals on the basis of their primary constitution discussed earlier, i.e., on the basis of the four primary elements and their qualities combined in contrarieties.

#### CLASSIFICATION OF ANIMALS AS SUGGESTED BY ARISTOTLE'S TREATMENT OF THEIR REPRODUCTIVE FACULTIES

##### 1. ORGANISMS WITH ONLY A VEGETATIVE FORM

###### A. Plants, reproduce by spontaneous generation, or come from seed.

<sup>1</sup> *H. A.*, 489b, 6.

<sup>2</sup> *De Gen. An.*, 758b, 9.

<sup>3</sup> *De ibid.*, 758b, 15 *et seq.*

<sup>4</sup> *De ibid.*, 758a, 33.

<sup>5</sup> *De ibid.*, 762b, 28.

<sup>6</sup> 1882, xxi-xxxiii.

- B. *Sponges*,<sup>1</sup> these are attached to a substratum and they are definitely plant-like, reproducing only by spontaneous generation. They are doubtfully sensitive.
- C. *Holothurians*<sup>2</sup> (sea-lungs, sea cucumbers). These are very similar to sponges, and are doubtfully sensitive.

## 2. ORGANISMS WITH SENSITIVE AND VEGETATIVE FORMS

These are intermediate between plants and animals, for they possess the characteristics of both. All are bloodless and sexless and correspond to our lower vertebrates.

- D. *Acalephae*<sup>3</sup> (sea-anemones, sea-nettles). Some of these are attached, some are free-living at times; all are definitely sensitive and imperfect forms reproducing by spontaneous generation.
- E. *Testaceans*<sup>4</sup> (or ostracoderms). These are imperfect forms which come into being by spontaneous generation, or by budding (as in mussels), or by giving off from themselves a generative slime (this is really spawn which Aristotle did not recognise as being made up of masses of eggs).

The divisions include the following sub-divisions:—

- |  |   |
|--|---|
| i. <i>Ascidians</i> . All these are attached and possess both hard and soft parts. |   |
| ii. <i>Sea-urchins</i> . These possess no soft parts and are free.                 |   |
| iii. <i>Univalves</i> (limpets, etc.)  | } iii, iv, and v possess both hard and soft parts, and are either free or attached. |
| iv. <i>Bivalves</i> (mussels, oysters, scallops, etc.)                             |   |
| v. <i>Turbinata</i> (whelks, purpuras)   |   |

## 3. ANIMALS

These are all free, void excrement, and are sensitive. They are divisible into two large groups depending on the presence or absence of red blood.

- (a) **Bloodless animals.** These are all imperfect and cold forms, and correspond to our higher invertebrates.

- F. *Insects*.<sup>5</sup> These are jointed animals reproducing characteristically by means of a scolex outside the body which becomes an egg (i.e., a pupa), or they reproduce by means of spontaneous generation producing male and female forms which can copulate giving rise to imperfect forms. We have already seen the subdivisions of the insects (page 22).

- G. *Malacostraca*,<sup>6</sup> or *Crustacea* (crab, lobster, shrimp, etc.). These are earthy animals which condition is indicated by their hard shells and they reproduce by means of imperfect eggs. Such eggs after being produced and laid increase in size. (Actually, such increase is only due to imbibition of water: the egg does not really develop any further unless fertilised. Aristotle, however, thought that this imbibition represented growth; hence the egg would then grow like a scolex, and so it was imperfect.)

<sup>1</sup> *H. A.*, 588b, 20; 548b, 27; *De Part. An.*, 681a, 17.

<sup>2</sup> *De Part. An.*, 681a, 17.

<sup>3</sup> *ibid.*, 681b, 1.

<sup>4</sup> *H. A.*, 528a, 1, to 531b, 19, etc.

<sup>5</sup> *De Gen. An.*, 732b, 13.

<sup>6</sup> *ibid.*, 755a, 14, and *H. A.*, 525a, 30 to 527b, 34.

H. *Malachia*<sup>1</sup> or *Cephalopods* (sepia, cuttlefish, etc.). All of these reproduce by means of an imperfect egg.

(b) **Blooded animals**, corresponding to our vertebrates.

α *Lower vertebrates* which comprise Aristotle's less perfect and less hot forms.

I. *Scaly, or bony Fishes*<sup>2</sup>, *Telosteans* (ordinary fishes). The members of this group are oviparous, laying an imperfect egg. When considering generation in fishes Aristotle in the *De Generatione Animalium*<sup>3</sup> leads us to infer that an egg is laid in an imperfect condition because there are too many of them in the uterus at once to allow of further internal development.

J. *Batrachus, The Frog Fish*.<sup>4</sup> This animal is oviparous, laying a perfect egg externally. Aristotle evidently considers this is an exceptional fish and, although he does not separate it off from the others, he was evidently in some doubt about its position, because in one place he includes it among the scaly fishes<sup>5</sup> while in another he puts it among the cartilaginous fishes.<sup>6</sup>

K. *Selachii*<sup>7</sup> or *Cartilaginous fishes*. These are the elasmobranchs, such as the sharks. They are oviparous because they are cold and viviparous because of their moisture,<sup>8</sup> and hence they are intermediate between birds and bony reptiles which are hot and dry. Being oviparous they produce a perfect egg internally, but they are externally viviparous for they rear the embryos externally. Aristotle knew that in the smooth-hound (*Mustelus laevis*) the young are connected to the uterus by means of a placenta and, as Platt<sup>9</sup> tells us in a footnote, this extraordinary fact was forgotten to be rediscovered only in 1840 by Muller.

L. *Serpents*<sup>10</sup> These, with the exception of the viper, are oviparous producing a perfect egg because of their heat, but they are dry, and hence it is only an egg. The viper is internally oviparous but externally viviparous like the *Selachii*.

M. *Oviparous quadrupeds*,<sup>11</sup> i.e., the reptiles (lizards, crocodiles, tortoises) and *Amphibia* (frogs and toads). These lay perfect eggs for they are perfect but cold. Curiously enough, Aristotle makes little, if any, reference to reproduction in the *Amphibia*. He knew frog spawn<sup>12</sup> and, as Platt points out,<sup>13</sup> he would scarcely consider frogs' eggs to be similar to reptilian eggs. *Frogs' eggs* should be classed with those of the bony fishes, and indeed Aristotle mentions them only in connection with those fishes.

<sup>1</sup> *H. A.*, 523b, 21, to 527b, 34.

<sup>2</sup> *De Gen. An.*, 755a, 8 et seq.

<sup>3</sup> *Ibid.*, 755a, 22.

<sup>4</sup> *Ibid.*, 754a, 25.

<sup>5</sup> *Ibid.*, 755a, 9.

<sup>6</sup> *Ibid.*, 754a, 25.

<sup>7</sup> *Ibid.*, 754a, 21; *H. A.* and many refs.

<sup>8</sup> *Ibid.*, 733a, 9.

<sup>9</sup> *Ibid.*, 754b, 35.

<sup>10</sup> *H. A.*, 511a, 14, and 558a, 25.

<sup>11</sup> *H. A.*, 558a, 1.

<sup>12</sup> *Ibid.*, 568a, 24.

<sup>13</sup> *Ibid.*, 568a, 24, footnote.

- N. *Birds*.<sup>1</sup> These are oviparous producing a perfect egg, although Aristotle considers that the young bird which hatches out is imperfect for, if the eyes of a young swallow are removed, new ones develop. Possibly by removal in this case he means great injury.<sup>2</sup> As in the scaly fishes here again the egg is perfect because the birds are warm but dry.<sup>3</sup>

(β) *Higher Vertebrates*, the most perfect animals, the hottest and the wettest.

- O. *Cetacea*<sup>4</sup> (whales and dolphins), which produce their young alive and directly, i.e., they are internally viviparous, and at least the dolphins and the porpoise are provided with milk for suckling their young.

- P. *Internally viviparous quadrupeds*,<sup>5</sup> such as horse, dog, cat, etc. All of them are hair-coated animals. They are viviparous from the very beginning, that is, they bring forth living young directly without the intervention of an egg stage. The mammalian ovum, of course, was unknown to Aristotle, neither could he have known about the oviparous quadrupeds or monotremes (duckbills, *echidna*).

- Q. *Man*, most perfect, viviparous biped.

## APPENDIX 3

### A SYNOPSIS OF LAMARCK'S CLASSIFICATION OF ANIMALS

#### A. FIRST STAGE OF ORGANISATION, INVERTEBRATES

Animals with no nerves, no vessels, no respiratory organs, no specialised internal organs except those for digestion.

*Class 1, Infusorians*. The most imperfect animals, most simply organised; they resemble plants in that they absorb food. The lowest is *Monas*, which was considered to be a speck of living matter, representing the starting point of the animal world.

*Class 2, Polypts*. Animals slightly better organised than the Infusorians; they have a definite shape and mouth.

#### B. SECOND STAGE OF ORGANISATION, INVERTEBRATES

These animals possess no nerves or vessels; they have some internal organs other than those for digestion.

*Class 3, Radiarians*. This class includes new types with a radial symmetry.

*Class 4, Worms*. The symmetry is now bilateral, from henceforth it remains so in all animals.

<sup>1</sup> *De Gen. An.*, 755b, 30.

<sup>2</sup> *Ibid.*, 744b, 30.

<sup>3</sup> An account of the growth of the chicken egg and of the development of the chick embryo will be found in *De Gen. An.*, 752a, 10 to 752b, 35; and *H. A.*, 561a, 6, to 562a, 20.

<sup>4</sup> *De Gen. An.*, 718b, 31; 732a, 30, and *H. A.*, 566b, 3.

<sup>5</sup> *De Gen. An.*, 718b, 28.

## C. THIRD STAGE OF ORGANISATION, INVERTEBRATES

These animals possess a longitudinal nerve cord; they respire by air-carrying tracheæ; the circulation is imperfect or absent.

*Class 5, Insects.* Among these there is shown an abrupt change from the worms. They have a distinct head, imperfect eyes, jointed legs and they possess characteristic wings; they copulate once only.

*Class 6, Arachnids.* Rather more perfectly organised than the insects; copulation occurs several times and they possess a rudimentary circulation.

## D. FOURTH STAGE OF ORGANISATION, INVERTEBRATES

These animals possess nerves ending in a longitudinal nerve cord, or in a brain without a spinal cord; they possess a circulation with arteries and veins.

*Class 7, Crustacea.* These are much more complex and perfect than previous animals. Respiration is not by means of tracheæ but by means of gills; the body is still jointed.

*Class 8, Annelids.* In these animals the articulations are disappearing; they possess arteries, etc., and gills.

*Class 9, Cirripedes.* These possess a shell or mantle; they have no head; the arms are jointed and they possess ganglia and longitudinal nerve cord.

*Class 10, Molluscs.* These animals are the most highly organised of invertebrates. They are the nearest to the fishes and seem to be intermediate between vertebrates and invertebrates in many respects.

## E. FIFTH STAGE OF ORGANISATION, VERTEBRATES

Among these animals the nerves end in a spinal cord and brain; they are cold blooded and the heart has a ventricle.

*Class 11, Fishes.* These animals are much more perfect than the molluscs. They are the first vertebrates, but still possess gills, have no eyelids, no voice; the articulations are all internal.

*Class 12, Reptiles.* Perfection has now reached a stage further which is seen in the appearance of rudimentary lungs; four limbs begin to appear.

## F. SIXTH STAGE OF ORGANISATION, VERTEBRATES

Among these there is a definite spinal cord and brain; they are warm blooded and the heart has two ventricles.

*Class 13, Birds.* The birds are more perfect still but they have no bladder, diaphragm or mammæ, and they are oviparous.

*Class 14, Mammals.* These are the most perfect animals. The mammals are viviparous, with mammæ; the legs are two or four jointed; the lungs are fully formed and the body possesses hair.

Man was placed by Lamarck in a separate class, the *Bimana*, because of his unique position and because he possessed an opposable thumb.

Later, about 1809, Lamarck considerably modified this arrangement in a single line starting with *Monas*, and ending with man. Instead he considered that the

series began from two groups, the worms and the infusorians, which arose spontaneously. The infusorians gave rise to the polyps and the radiarians, while the worms produced all the remaining classes in an indirect way. His newer classification, the connecting links of which were arranged like the branches of a tree joined to one of two trunks, was altogether more reasonable, for it accounted for several dead ends. Years later the construction of genealogies of this type became the popular pastime of some of the Darwinians and of Haeckel.

## APPENDIX 4

### A FACTORIAL ACCOUNT OF ONE OF MENDEL'S EXPERIMENTS

Plants and animals possess reproductive tissues called *germ plasma* which produces sex cells or *gametes*. On fertilization a male gamete unites with a female gamete in such a way that each loses its own individuality, producing a single cell, the product of fusion, called a *zygote*. In the course of time the zygote develops to produce an embryo and this an adult organism. Mendelism is concerned only with inheritance resulting from *sexual reproduction*, i.e., reproduction by union of male and female gametes. It is postulated that in the gametes of the organisms concerned there occur *factors* or *genes* which represent characters in the young and adult organisms. The law of segregation refers to the separation of those factors which came in from one sex from those which came in from the other. This segregation takes place during the formation of the gametes in the germ plasma, and the various factors are randomly assorted in the gametes. The law of recombination refers to the coming together of the factors in the zygote when fertilization takes place.

To describe an experiment factorially we can represent the original parental generation by  $P_1$ , the first hybrid by  $F_1$ , the second hybrid generation by  $F_2$ , and so on. One of Mendel's experiments was as follows:—

$P_1$	Pure tall plant	×	Pure dwarf plant
$F_1$		all tall	
		$F_1 \times F_1$	
$F_2$		3 tall : 1 dwarf	

If now we represent the factor for tallness by  $T$ , then each pure tall plant will receive a  $T$  from each of its parents, and so can be written as  $TT$ . Likewise we can represent the factor for dwarfness by  $t$  then each pure dwarf plant can be written as  $tt$ .

Factorially the cross of the  $P_1$  generation is:—

$$TT \times tt$$

According to the law of segregation, when the gametes are being formed that which came in from one parent segregates from that which came in from the other parent, i.e.,  $T$  separates from  $T$  and  $t$  from  $t$ . Hence the gametes can be written as  $T$  and  $t$ . When fertilization occurs these gametes unite. The  $F_1$  generation is then written as  $Tt$ . Here we see the tallness is dominant to dwarfness which is recessive. The hybrid is written as  $Tt$ , therefore, whenever a  $T$  appears, the plant will be tall. According to this system there are obviously two kinds of tall plants as follows:—

- $TT$  which, because they contain only  $T$ , are said to be homozygous, or a homozygote. These breed true.
- $Tt$  which, because it contains two unlike factors, is said to be heterozygous or a heterozygote. These are hybrids.

This notation enables us to see why  $Tt$  is a hybrid. On reproduction the  $T$  from one parent will separate from the  $t$  from the other, and so two kinds of gametes will be produced in equal numbers, i.e.,  $T$  and  $t$ . Thus  $Tt$  is a hybrid because it produces *dissimilar* gametes. In order to distinguish between these two types of tall plants two new words are necessary, namely *phenotype* and *genotype*. What an organism *looks like* is called its *phenotype*, but what an organism *is* in its germ plasm is called its *genotype*. Thus  $TT$  and  $Tt$  are phenotypically alike but genotypically unlike.

To get the  $F_2$  generation two of the  $F_1$  hybrids are crossed:

$$Tt \times Tt$$

the gametes will be:

$$T, t \text{ and } T, t$$

When fertilization occurs these gametes recombine in all possible ways, the male from one plant with the female from the other, giving the following result:

$$TT, Tt, Tt, tt$$

We have seen that wherever  $T$  occurs the plant will be tall, hence this result may be interpreted as:  $TT$  (tall) : 2  $Tt$  (tall),  $tt$  (dwarf) or 3 tall : 1 dwarf. In the  $F_2$  generation it is easy to see that:  $TT$ , being homozygous, will give nothing but tall plants;  $tt$ , being homozygous, will give nothing but dwarf plants;  $Tt$ , being heterozygous, will again split up into tall, dwarfs and hybrid tall, i.e., it will again repeat the 3 : 1 ratio of the  $F_1$ .

The theoretical results obtained by the use of the symbols fit in perfectly well with the actual experimental results. Hence we are justified in using this short-hand method as an aid in the interpretation of our experimental results. In each of the pairs of contrasting characters which Mendel took he found that one of them was dominant and the other recessive. If  $T$  represents the factor for tallness and it is dominant, then the factor for dwarfness is usually written with the small letter, i.e.,  $t$ , this factor is the *allelomorph* of  $T$  and it is recessive. Actually Mendel's results regarding dominance were exceptional, for the  $F_1$  hybrid is more usually intermediate in phenotypic expression between the parents for each pair of characters. Mendel noticed, however, that the  $F_1$  hybrid was often more abundant in its growth than either parent; this is a phenomenon which we now call *heterosis*, or hybrid vigour, and it is made use of economically. It is easy to see that if dominance is absent then the 3 : 1 ratio becomes a 1 : 2 : 1 ratio.

Confirmation of the theoretical explanation implied in this factorial system is given by backcrossing the  $F_1$  hybrids, i.e., by breeding them back on to the  $P_1$  parents.

(a) *Backcross on to the dominant parent:*

$$\begin{array}{lcl} & TT & \times \quad Tt \\ \text{gametes:} & \text{all } T & T \text{ and } t \\ \text{zygotes:} & TT & Tt \end{array}$$

i.e., all tall, which is actually obtained.

(b) *Backcross on to the recessive:*

$$\begin{array}{lcl} & tt & \times \quad Tt \\ \text{gametes:} & \text{all } t & T \text{ and } t \\ \text{zygotes:} & Tt & tt \end{array}$$

i.e., 1 tall : 1 dwarf, which is actually obtained.

The experiments given above refer to the *monohybrid* ratio, where only one pair of characters is used. The *dihybrid* ratio, where two pairs of contrasting



characters are used, is given below, using tall and dwarf as one pair, and red and white flower colour as the other. Tall and red are dominant to dwarf and white. If *T* represents tall, *t* dwarf, *R* red, and *r* white, then the first parental generation cross can be written as:

$$P_1 \quad \begin{array}{c} \text{tall red plant} \\ TTRR \end{array} \times \begin{array}{c} \text{dwarf white plant} \\ ttrr \end{array}$$

In each pair of factors segregation occurs, but the factors of different pairs assort at random, hence

$$F_1 \text{ gametes will be: } \begin{array}{c} TR \\ TtRr \end{array} \quad \begin{array}{c} tr \\ TtRr \end{array}$$

$$F_1 \text{ zygotes: } \begin{array}{c} \text{tall and red} \\ F_1 \times F_1 \\ TtRr \times TtRr \end{array}$$

the gametes will be of four different kinds in each sex:

$$TR, \quad Tr, \quad tR, \quad tr$$

In order to get the possible  $F_2$  zygotes the recombination of these gametes can be done quickly by means of the checkerboard method, as shown in Table 11.

Table 11  
Checkerboard method of determining  $F_2$  zygotes

		$F_2$ Eggs			
		TR	Tr	tR	tr
Pollen.	TR	TTRR	TTRr	TtRR	TtRr
	Tr	TTRr	TTrr	TtRr	Ttrr
	tR	TtRR	TtRr	ttRR	ttRr
	tr	TtRr	Ttrr	ttRr	ttrr

If we collect these zygotes in Table 11 together we get:

- 1 *TTRR*, 2 *TTRr*, 2 *TtRR*, 4 *TtRr*, i.e., 9 tall and red.  
 1 *TTrr*, 1 *Ttrr*, 1 *Ttrr*, i.e., 3 tall and white.  
 1 *ttRR*, 1 *ttRr*, 1 *ttRr*, i.e., 3 dwarf and red.  
 1 *ttrr*, i.e., 1 dwarf and white.

This ratio of 9 : 3 : 3 : 1 agrees with experimental results. We notice that two new combinations of characters have occurred, i.e., tall plants with white flowers and dwarf plants with red flowers. In each case one of them is pure-breeding; these are *TTrr* and *ttRR*. Thus two new races have been produced. This production of new races can be made use of to produce desirable strains of economic plants and animals.

## APPENDIX 5

EXAMPLES OF GENETICAL EXPERIMENTS AND APPLICATIONS  
WORKED OUT STATISTICALLY<sup>1</sup>*Experiments with Drosophila**Example 1*Experiment 1. *Investigation of the sex ratio*

In this experiment a wild type female *Drosophila* + ♀ (in American notation the wild type gene is indicated by the plus sign, +) was placed in a culture bottle with a male showing the mutant character *Curled* (Cu ♂). In this type the wings are appreciably curled upwards, while in the normal insect they are flat. The first generation, or  $F_1$ , flies of this cross all resemble the wild type, thus showing that the wild type character, normal wing, is dominant, and Cu recessive. Table 12 shows the results obtained in  $F_1$ .

+ ♀ crossed with Cu ♂  
 $F_1$  +

Table 12

*Results showing sex proportion in  $F_1$* 

Experiment	Number of females	Number of males	Total
1	18	20	38
2	28	25	53
3	19	11	30
4	28	29	57
5	15	15	30
6	11	9	20
7	18	15	33
8	37	36	73
9	31	30	61
10	18	18	36
11	18	20	38
12	18	20	38
Total	259	248	507

Theoretically the number of the sexes should be equal. Thus with the total of 507 flies in  $F_1$  the normal ratio should be 253.5 : 253.5. In other words, the results deviate from the expected ratio by 11. The next step is to find out whether or not this deviation is significant. To do this we use the formula,  $\text{Dev.} = \pm .6745 \sqrt{npq}$ , where  $n$  = the total number of individuals,  $p = \frac{1}{2}$ , and  $q = 1-p = \frac{1}{2}$ ;  $p$  and  $q$  represent the ratio expressed as a vulgar fraction when the expectation is 1 : 1.

Hence we get:

$$\begin{aligned}\text{Dev.} &= \pm .6745 \sqrt{\frac{1}{2} \times \frac{1}{2} \times 507} \\ &= \pm .6745 \sqrt{126.75} \\ &= \pm 7.6\end{aligned}$$

<sup>1</sup> This is reprinted from an article "Experimental Genetics in Schools," by Fothergill, 1939, pp. 19-24.

This means that if we take 507 individuals at random from the progeny of the above cross, then we may get deviations as great as 7.6 from the expected ratio of 1 : 1. Actually, of course, our results are not significant, because of a time limit which was introduced into the experiment. All the eggs will probably have hatched out, but all the insects may not have emerged from the pupa stage. As the female of *Drosophila* develops quicker than the male, then under these circumstances we would expect an excess of females over males. Such an excess was obtained.

Experiment 2. *To investigate the monohybrid ratio*

F<sub>1</sub> flies are all of the wild type. To get the F<sub>2</sub> ratio these were inbred—that is, crossed among themselves. The results are given in Table 13.

Table 13  
*Results of the F<sub>2</sub> generation*

Experiment	Number of + flies	Number of <i>Cu</i> flies	Total
1	66	22	88
2	57	19	76
3	83	28	111
4	112	33	145
5	136	42	178
6	103	34	137
7	109	36	145
8	48	15	63
9	84	28	112
10	87	29	116
11	87	30	117
12	123	41	164
Total	1,095	357	1,452

The proportion of + and *Cu* flies in F<sub>2</sub> suggests that the ratio is 3 + : 1 *Cu*. The expected ratio with 1,452 as the total number of flies is then 1,089 + : 363 *Cu*, but the actual ratio obtained was 1,095 + : 357 *Cu*. Therefore the deviation obtained is 363—357 (or 1,095—1,089), which is 6. Again, is this deviation significant?

Dev. =  $\pm .6745\sqrt{npq}$ , where  $n$  = total number of individuals,  $p = \frac{1}{4}$ ,  $q = 1 - p = \frac{3}{4}$ , because the expected ratio is 3 : 1,  $p : q$ .

$$\begin{aligned}\text{Hence Dev.} &= \pm .6745\sqrt{1 \times \frac{1}{4} \times 1,452} \\ &= 9.66\end{aligned}$$

Hence 9.66 is the true deviation, and if our result falls within this figure it will be significant. It does, and thus our ratio reduced to the lowest value is a simple 3 : 1, showing that the characters are inherited in a simple Mendelian fashion.

Example 2

This example is more complicated than the first, and has been chosen to show a method by which crossing-over can be used to find the sequence and distances

apart of genes which are known to be on the same chromosome. An experiment of this type, in which three characters are used to determine the locus of several genes, is called a *three-point experiment*. It could also be done in three separate experiments by investigating the inheritance of the three characters taken two at a time, i.e., first dusky-singed, second dusky-ruby, third singed-ruby. The chances of error in the results would obviously be greatly increased by using the latter method.

The characters dusky (*dy*), singed (*sn*) and ruby (*rb*) are known to occur on the first, or *X*, chromosome of *Drosophila*. The wing of the mutant dusky is darker than that of the normal (or  $\frac{+}{+}$ ) fly, and is about four-fifths the normal size. Singed is a mutant showing twisted and bent hairs and bristles. In one type of this form the female is sterile, while in another it is completely fertile.<sup>1</sup> The normal fly has red eyes, while ruby mutant possesses pink and transparent eyes. All of these three types are recessive to the normal conditions.

### Experiment 3. To show the occurrence of crossing-over

The following cross was made:

Dusky, singed  $\times$  ruby  
i.e.,  $dy\ sn\ \frac{+rb}{+}$   $\times$   $\frac{+dy}{+}\ \frac{+sn}{+}\ rb$

$F_1$  then is

$\frac{dy}{+dy}$	$\frac{sn}{+sn}$	$\frac{+rb}{rb}$
------------------	------------------	------------------

All of these characters are recessive to their wild type allelomorphs, hence the  $F_1$  will be wild type in appearance. The  $F_1$  female was then crossed with the triple recessive (i.e., *dy sn rb*).

$F_1\ \frac{dy}{+dy}\ \frac{sn+rb}{+sn}\ \frac{rb}{rb}$  female  $\times$   $dy\ sn\ rb$  male

The results of the  $F_2$  are shown in Table 14 below.

The genes controlling the expression of these characters are known to be on the *X* chromosomes. Thus the original chromosomes that went into this cross were two *X*s, each bearing  $\frac{dy\ sn\ +rb}{+}$  from the female and one *X* and *Y* from the male. The *X* chromosome of the male carries the gene for ruby (*rb*) and, of course, the wild type allelomorphs of *dy* and *sn* as  $\frac{+dy\ +sn\ rb}{+}$ . As these chromosomes are homologous, when meiosis occurred they would conjugate. Hence to produce the combinations shown in Table 14 crossing-over must have taken place. This is illustrated by the accompanying diagram (Figure 7).

Thus the percentage of occurrence of these new combinations gives an estimate of the amount of crossing-over which has occurred in order to produce them. Present in the progeny of this cross are two classes, identical with the parent strains, and six classes in which the three pairs of allelomorphs appear in every possible combination, but which fall into three complementary pairs. To calculate the amount of recombination (representative of the distance) between the loci in this experiment and find their relative position on the chromosome, we have to consider the crossing-over between any two pairs of allelomorphs.

<sup>1</sup> Morgan, Bridges and Sturtevant, 1925.

Table 14  
F<sub>2</sub> Results of Experiment 3

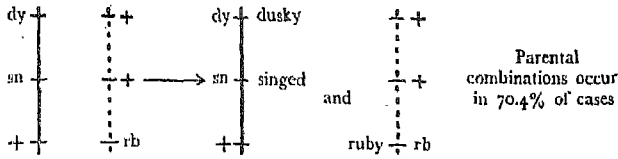
Classes	Phenotype	Genotypes	No. of flies	Total No. per class	Combinations			Frequency
					dy - rb	dy - sn	sn - rb	
Non cross-overs	dusky-singed	dy sn +rb	143	285				70.4%
	ruby	+dy +sn rb	142					
Single cross-overs	dusky-ruby	dy +sn rb	21	55	114	61		28.3%
	singed	+dy sn +rb	34					
Single cross-overs	dusky-singed-ruby	dy sn rb	24	59			64	15.8%
	wild type	+dy +sn +rb	35					
Double cross-overs	ruby-singed	+dy sn rb	1	6				15.6%
	dusky	dy +sn +rb	5					

Total No. of flies, 405.

Phenotype = the external appearance of the insect.

Genotype = the genic expression of the germ plasm of the organism.

## A Without Crossing-over



## B With Crossing-over

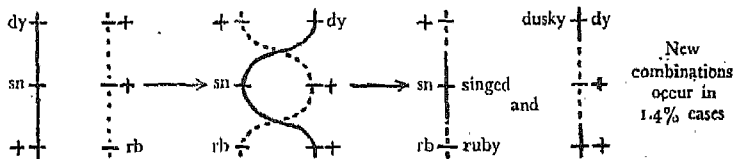
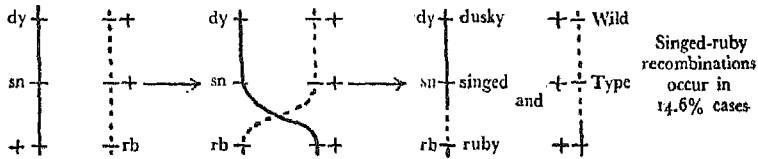
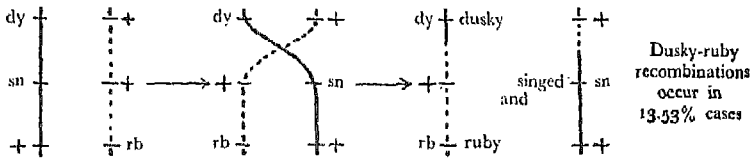
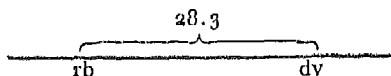


Figure 7. Legend

Diagrammatic interpretation of the results of experiment 3

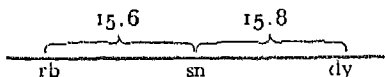
This diagram illustrates how, by crossing-over at the points shown, we get the various combinations of the characters dusky (*dy*), singed (*sn*), and ruby (*rb*), which were actually obtained in experiment 3. The parental chromosomes concerned are shown on the left: one of them is represented by a continuous line, the other by an interrupted line. In A no crossing-over occurs, hence the parental combinations of characters are obtained. In B, crossing-over occurs at the points shown in three ways; the resultant zygotes are shown on the right. The sign + (plus) indicates the presence of the wild type of gene. For simplification the chromatids are omitted. (After Fothergill, *Biology*, 5, 23, 1939.)

The two recessives dusky and ruby entered the experiment separately. They came together in both single cross-over classes. Their recombination value is 28.3%. This may be represented graphically :



The two recessives dusky and singed entered the cross together. They separate in the first single cross-over class and in the double cross-over class. The sum of these two classes gives a recombination value of 15.6%, singed is therefore 15.6 units away from dusky, but its position in relation to ruby is doubtful. It may either be situated between ruby and dusky or on the other side of the latter.

The analysis of the recessives ruby and singed provides the answer. They entered the experiment separately and are being brought together in the second single cross-over class and in the double cross-over class. Their recombination value is 15.8%. Thus the locus of *sn* is practically equidistant between *rb* and *dy*. The genetic chromosome map thus becomes :



## APPENDIX 6

### SOME FURTHER LAMARCKIAN EXPERIMENTS

Some references to the earlier reported successful Lamarckian experiments not included in the text are given below in chronological order:—

J. T. Cunningham (1893, 1895-97) on *Flatfishes*.

A. Hyatt (1894) on *Planorbis*.

M. Standfuss (1898) on *Vanessa*.

G. Ferronière (1901) on *Tubifex*.

E. Fischer (1902, 1907) on *Aretia carya*.

V. L. Kellogg and R. G. Bell (1903) on *Mulberry Silkworm*.

(and see Kellogg *Darwinism Today* (1907), appendix to chapter X, pp. 298-304).

V. L. Kellogg (1904) on *Philosomia*.

W. L. Tower (1907) on *Chrysomelid beetles*.

R. Woltereck (1908, 1911, 1928) on *Daphnia*.

A. Pictet (1910) on *Lymantria*.

W. E. Agar (1913) on *Simonecephalus vetulus*.

P. Kammerer (1923) on *Ciona*.

A. C. Wladimirsky (1928) on *Plutella*.

Rather more detailed accounts of some later Lamarckian experiments are now given.

(1) C. Schroder (1903) on *Gracilaria*

Schroder found that the larva of *Gracilaria stigmatella* (the willow moth) makes a cocoon by bending over the tip of a leaf and fixing it with its web. Schroder then cut off the tips of the leaves with the result that the larvæ rolled over the lateral edges and he reported that this new habit was inherited for several generations.

He also fed the larval of *Phytora vitellina* (the willow beetle), which normally lives on smooth leaves, on hairy leaves for several generations until the new habit was acquired. He stated that this habit was then inherited.

(11) *M. F. Guyer and E. Smith*

Guyer and Smith<sup>1</sup>, besides claiming to have provided evidence for the inheritance of acquired characters, were also able to suggest the possible mechanism for the transmission of these characters. They took the eye lenses of freshly killed rabbits, pulped them in a mortar, added saline solution and then injected small quantities of the resultant decoction either intravenously or interperitoneally in fowls. These injections were repeated weekly for several weeks. Theoretically, the injected eye lens decoction would induce the formation of anti-bodies to rabbit-eye lens in the blood serum of the fowl. These anti-bodies should prohibit or interfere with the formation of normal lenses in the rabbit. They then took the blood serum of the treated fowl and injected it several times into the bodies of pregnant rabbits at the estimated important period in the development of the embryonic eye lens. Some mother rabbits and some embryos died but 61 young were obtained, and of these 4 had one or both eyes defective while 5 of them had abnormal eyes. Some of the apparently normal young rabbits later produced descendants with defective eyes. The defects were of various kinds but were probably due to the early injury of the eye lenses. In several hundred control rabbits injected with unsensitized fowl-serum not one young rabbit showed eye defects.

The important point about these experiments is that the eye defects, once induced, were passed on by inheritance for 8 or 9 generations. Further, the defects got worse in succeeding generations. Later Guyer and Smith destroyed the lenses of living rabbits and thereby induced the formation of anti-bodies which prevented the development of normal eyes in some embryos. These eye defects were also inherited. Guyer and Smith consider that their work shows that definite serological reactions can be induced in foetuses through the active co-operation of the somatic tissues of the mother. "With facts such as these before us, is it not a rational hypothesis to assume that changes in various parts of a body may on occasion influence the representatives of such parts in the germ cell borne by that body?" Guyer remarks further: "May we not surmise then that as regards inheritance and evolution, Lamarck was not wholly in error when he stressed the importance of use and disuse of a part, or of modifications due to environmental change, in altering the course of the hereditary stream, particularly if we conceive of the influences as being prolonged, possibly over many generations? Have we not in the serological mechanism of the body of animals an adequate means for the incitement of the germinal changes which underlie certain aspects of evolution?" However, similar experiments to those of Guyer and Smith were performed by Silfäst,<sup>2</sup> Huxley, J. S., and Carr-Saunders,<sup>3</sup> and Finlay<sup>4</sup> with dissimilar results.

(111) *B. Dürkhen (1923) and J. W. Heslop Harrison (1928b) on Pieris*

In *Pieris brassicae* (the cabbage white butterfly) the skin of the pupa is dirty white in colour but the blood is coloured green. Hence, if the skin becomes colourless the green colour of the blood shines through and the pupa looks as if it were green. Normally about 4% of the pupæ of the cabbage butterfly are green. Dürkhen placed caterpillars of this species in boxes with orange coloured glass lids, and found that 69% of the resulting pupæ became green. When

<sup>1</sup> 1918, 1920, 1921, 1922.

<sup>2</sup> 1922.

<sup>3</sup> 1924.

<sup>4</sup> 1924.



caterpillars of the next generation appeared, half of them were reared under normal light conditions and these gave rise to 41% of green pupæ. The other half were reared under orange light again, and 95% green pupæ resulted. As MacBride<sup>1</sup> says: "These experiments show clearly that when a habit is acquired by one generation, a second generation exposed to the same conditions acquires the same habit more quickly and thoroughly; and that when the offspring of a generation which has acquired a peculiar habit are returned to normal and typical conditions they still show the effects of the habits acquired by the parental generation."

Heslop Harrison repeated and confirmed Dürkhen's work, but he used *Pieris napi* instead of *P. brassicae*. Harrison reared the caterpillars in three types of cages as follows: (a) under window glass, (b) under blue glass, and (c) under orange glass. He found that in (a) the controls 20.9% of the resulting pupæ were green, in (b) there were 21.9% green pupæ, while in (c) there were 93.4% green pupæ. It is interesting to note that the percentage of green pupæ obtained under white and blue light was essentially the same. The pupæ from the blue glass cage were then destroyed. In the next generation the controls produced the normal 21% of green pupæ, but those under orange glass gave 95.2% of green pupæ. The controls were then destroyed, but the green pupæ of the second generation were reared under the normal light conditions, and 31 pupæ were obtained, which were all green: this was an unexpected result.

Half of the pupæ emerged normally, but the other half showed delayed emergence. Heslop Harrison then reared one lot under a variety of conditions, such as on red tile, on glass, on perforated zinc, etc. Under these conditions the percentage of green pupæ was 58. The other lot of third generation caterpillars were reared under black glass and 94.6% green pupæ were obtained. Heslop Harrison concludes that "... there can be no doubt that the green pupæ colour, induced by the inhibition of pigment by the use of orange light, is inherited, *no matter how*. In other words, ample confirmation has been obtained of Dürkhen's and of Brecker's<sup>2</sup> work."

While a certain amount of selection may have obtained in both Dürkhen's and Heslop Harrison's experiments, the percentages are much too high, especially in the latter's work, to be explained on a basis of selection alone. Hence, Robson and Richards,<sup>3</sup> who have criticised most modern experiments of this type, can but say: "We believe a *prima facie* case has been made out for the inheritance of this modification."

#### (iv) Metalnikov on *Galleria* (1924)

Metalnikov worked on a moth, *Galleria*, the larvæ of which he subjected to the action of the cholera bacillus *Vibrio* and the immunizing vaccine. Metalnikov started with a single female specimen of *Galleria* which produced caterpillars. Half of the caterpillars received a dose of vaccine, half were untreated, and the whole lot were infected with *Vibrio*. Those that survived were made the parents of the next generation and the process of inoculation was repeated for several generations. In each generation the resistance to the bacillus, i.e., the immunity, increased until in the ninth generation 75% of the insects were immune. If selection alone were acting it would be expected to reach a maximum beyond which further selection would be ineffective. According to MacBride<sup>4</sup> Metalnikov's work is one of the best examples of a Lamarckian effect, whereas Robson and Richards<sup>5</sup> consider the experiments are inconclusive.

<sup>1</sup> 1931, p. 941.

<sup>2</sup> 1923.

<sup>3</sup> 1936, p. 38.

<sup>4</sup> 1931, p. 941.

<sup>5</sup> 1936.

## APPENDIX 7

## AN ACCOUNT OF MULLER'S TECHNIQUE FOR RECOGNISING MUTATIONS AND FOR MEASURING THE MUTATION RATE.

In a paper published after but written before his paper announcing the successful production of X-ray mutations in *Drosophila*, Muller<sup>1</sup> gave a detailed exposition of the need for suitable methods of measuring the mutation rate, and he described his own technique which he meant to use in investigating the effects of temperature on the mutation process. It was this technique, developed by experience from work begun in 1918, which enabled him to recognise small mutations in *Drosophila* induced by means of X-rays. The occurrence of spontaneous mutations had indicated that they were rare events, occurring about once in 50,000 flies, so that a mere counting of broods of flies and the possible mutations among them was practically useless for estimating rates of mutation with any degree of accuracy.

To estimate rates in this way would be "like making graphs to show the rates of occurrence of gold pieces on streets of different types," as Muller puts it.<sup>2</sup> Muller points out that, on theoretical grounds, lethal mutations should be of more frequent occurrence than the ordinary "visible" mutations, and so he set about devising indirect methods of estimating the rate of their production which could be used as a measure of the mutation rate generally. He says: "It has been the chief aim of the present writer's work during the past 8 years to develop a technique that will overcome these difficulties and, by the use of it, to obtain decisive counts that would establish the effectiveness, or the non-effectiveness within normal limits, of some important environic influences in modifying the rate of gene mutation. It is believed that this object has at last been definitely achieved, and that the data so obtained in the first place furnish information of theoretical (perhaps ultimately of practical) value, and in the second place, demonstrate the general usefulness of the method for an unlimited amount of further work on the rate of gene mutation under varying external and internal conditions."<sup>3</sup> Muller's words proved to be true, and his technique has become the standard for the detection and investigation of the mutation rate. His chief basic methods are elaborations of Morgan's<sup>4</sup> method of showing the presence of a new lethal gene and they are given below.

(i) *The ClB Technique*

This technique measures the lethal mutation rate in X-chromosomes and, although it is used most extensively on *Drosophila*, it can be applied to any organism with a similar sex chromosome mechanism. The method depends on the movements of the X-chromosome in the male which can be traced from generation to generation.

Males which bear known genes, called markers, on their X-chromosome, are placed in gelatine capsules and exposed to the action of X-rays, the dosage of which can be varied. These rayed males are then crossed with females with two X-chromosomes one of which carries C, a gene suppressing crossing-over between the X-chromosomes, *l* a lethal recessive gene, and *B*, or bar, a dominant eye gene. If in F<sub>2</sub> of this cross no males are produced, it may be inferred that a lethal mutation arose in the original X-rayed males. The method is best shown diagrammatically (see Figures 8 and 9).

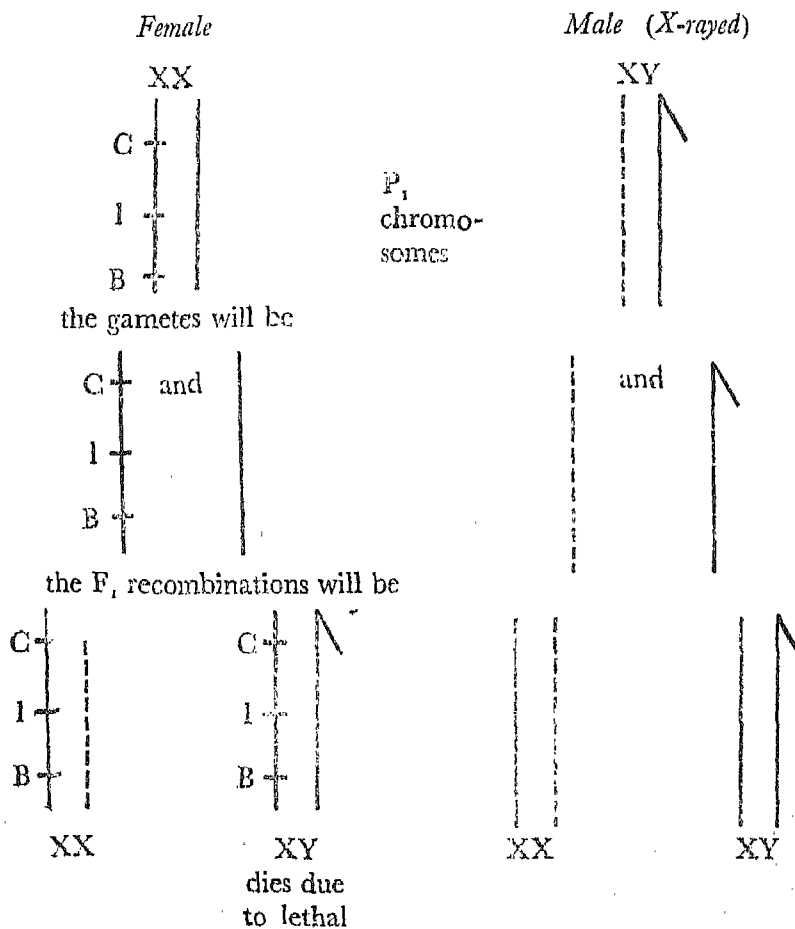
<sup>1</sup> 1928b.

<sup>2</sup> 1928b, p. 283.

<sup>3</sup> 1928b, p. 285.

<sup>4</sup> 1912.

Figure 8

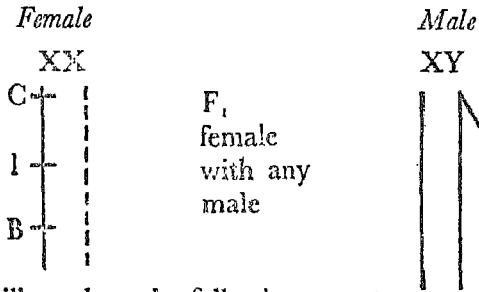
The *ClB* Method of Mutant Determination (1st cross)

In the above diagram I represents a lethal gene, B represents the dominant bar-eye gene and C represents a dominant cross-over suppressor. Chromosomes are represented by lines, the X-rayed X chromosome of the male by a broken line. In *Drosophila* females possess two X chromosomes and males one X and one Y each.

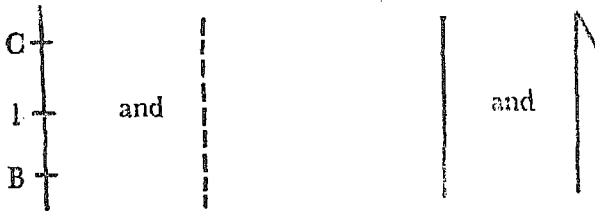
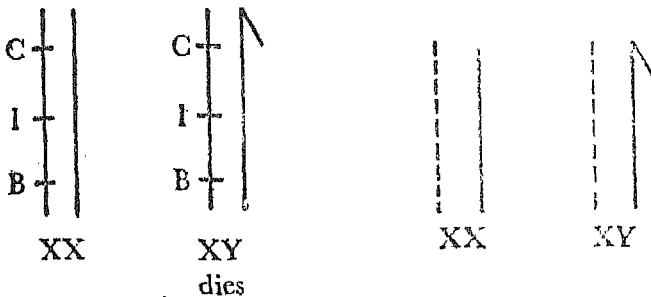
The female C I B contains a rayed X chromosome from the

P<sub>1</sub> male parent and it is recognisable by inspection because it also carries the dominant gene B (bar eye). This female is then crossed to any male.

Figure 9

*The ClB Method of Mutant Determination (2nd cross)*

these will produce the following gametes

 $F_2$  recombinations will beIn the  $F_2$  generation the  males will die because they will

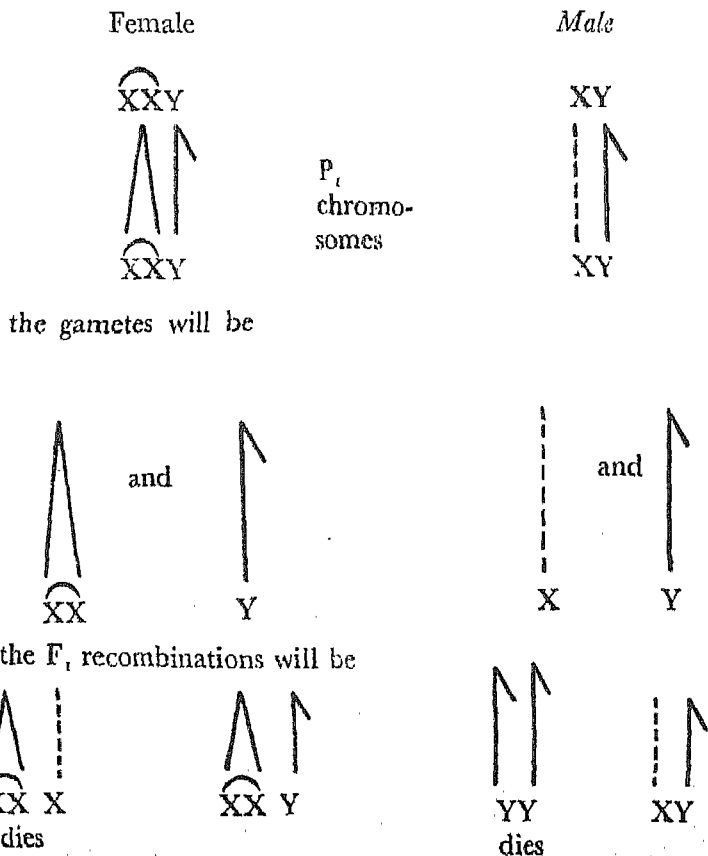
contain a lethal gene (*l*) which is not balanced by any allelomorph in the *Y* chromosome which is inactive. The other males will survive and the ratio would be 2 females : 1 male *unless a new lethal mutation arose in the - - - or X* (X-rayed) chromosome, of the original rayed male. If this occurred, then these males would die also and the sex ratio in  $F_2$  would be all females and no males.<sup>1</sup>

<sup>1</sup> The 2 females : 1 male ratio is itself evidence of the presence of a lethal which in this case we have deliberately used, i.e. the lethal gene *l*.

(ii) *The Attached X Method*

This method is used for showing the production of new visible mutations in X-rayed males. A stock of female *Drosophila* has been produced which possesses 2 X chromosomes fused at or near to one end (the spindle fibre end) and also a Y chromosome, i.e., it can be written down as  $XXY$ . Such flies are called attached Xs. To determine visible sex-linked mutations X-rayed males are crossed with attached X females and the results show if any new mutations have arisen as shown diagrammatically in figure 10.

Figure 10

*The Attached X Method of Mutant Determination*

The female with three Xs in figure 10 is a super female and will either be sterile or will die; the male with 2 Ys and no X chromosomes dies. In  $F_1$  here the only living males, namely  $XY$ , will have obtained their X chromosome from their father and any visible mutation produced in it by the action of the rays on the original  $P_1$  will show on it.

(iii) *Method of Accumulation of Autosomal Lethals*

This method can be used for the detection of non-visible mutations (lethals) which are borne on the autosomes (that is on the chromosomes other than the sex chromosomes). It is a very laborious method and the genetic structure of the organism on which it is being used must be well known.

Most mutants when they appear are recessive to the normal condition, and thus occur as heterozygotes associated with the dominant normal allelomorph. If this new gene occurs on an autosome, individuals showing the new phenotypic effect produced by the new gene can only arise by the crossing of suitable heterozygotes for the mutant and even so they will be produced in the proportion of 1 mutant phenotype to 3 normal phenotypes. The experimental work to extract such new homozygous mutants would involve great labour. Muller then set out to devise a method of accumulating new mutant genes for several generations before actually testing for them. He began the experiment with a stock known to contain no mutant genes and bred from these for several generations, i.e., to the  $F_n$  generation. Individuals from the  $n$ th generation were then tested for mutant genes by breeding them to  $F_{n+1}$  and  $F_{n+2}$  generations in a certain way. In order that this method should give a record of all new mutants arising during the  $n$  generations, it was necessary to counteract the effect of germinal selection of lethals arising in the cultures. Muller did this by starting with stock which already contained what are called "balanced lethals" deliberately introduced. Here two different lethals were introduced by breeding methods into the chromosome of a homologous pair at different loci. As long as inbreeding of this stock is carried out, then, in this pair of chromosomes, these lethals would always be present in heterozygous form; new lethals appearing on these chromosomes will not then be subjected to any germinal selection. The chromosomes used by Muller were also furnished with the gene  $C$  which prevented crossing-over. After various modifications the method of detecting mutations was worked out as shown diagrammatically below (see figures 11 and 12). The balanced stock flies can be represented by

$$\begin{array}{ccccccc} & T & & b & c & p & a & m \\ \hline Cy & l & & C & & & cn_2 & \end{array}$$

where  $Cy$  represents the gene for dominant curly wing,  $T$  the gene for recessive dumpy abdomen,  $b$  the gene for recessive black body colour,  $l$  a lethal gene,  $c$  the gene for curved wing,  $C$  the cross-over inhibiting gene,  $p$  the gene for recessive purple eye colour,  $cn_2$  the gene for cinnabar eye colour,  $a$  the gene for arc wing, and  $m$  the gene for morula eye causing sterility in the female which thus acts as a partial lethal. In some of the experiments the gene  $S$  for star eye was made use of; this has a dominant effect on the eye, but a recessive lethal effect.

The chromosome to be tested for new mutations occurring after treatment with rays is

$$\begin{array}{ccccccc} & T & & b & c & p & a & m \\ \hline & & & & & & & \end{array} \quad \text{its homologue is} \quad \begin{array}{ccccccc} Cy & l & & C & & & cn_2 \\ \hline \end{array}$$

After treatment, such as with X-rays, this stock is inbred for several ( $n$ ) generations, resulting in the production of a number of ( $F_n$ ) lines. A male is taken from each of these lines and bred from in a particular way, (a) it is outcrossed to some female, of known and chosen composition, namely

$$\begin{array}{ccccccc} S & T & & b & c & p & a & m \\ \hline Cy & l & & C & & & cn_2 & \end{array}$$

to give the  $F_{n+1}$  generation, and (b)  $F_{n+1}$  flies which now contain the test chromosome (these are visible by inspection of phenotypic characters) are bred among themselves to give the  $F_{n+2}$  generation. The multiple recessive flies among this generation will be those expected to show any new mutant characters which might arise. If this character is controlled by a lethal gene none of the multiple recessives will be obtained (see figure 11).

Figure 11

*The Production of the  $F_{n+1}$  Generation*

$$\begin{array}{c}
 F_n \text{ test male} \\
 \hline
 \text{Cy} \quad \text{T} \quad \text{b c p} \quad \text{a m} \\
 \quad \quad \text{l} \quad \text{C} \quad \text{cn}_1
 \end{array}
 \times
 \begin{array}{c}
 \text{Female of known composition} \\
 \hline
 \text{Cy} \quad \text{T} \quad \text{b c p} \quad \text{a m} \\
 \quad \quad \text{l} \quad \text{C p} \quad \text{cn}_2
 \end{array}$$

the gametes will be

$$\begin{array}{c}
 \text{T b c p a m} \\
 \hline
 \text{Cy l C cn}_2
 \end{array}
 \text{ and }
 \begin{array}{c}
 \text{S T b c p a m} \\
 \hline
 \text{Cy l C p cn}_2
 \end{array}$$

the  $F_{n+1}$  combinations will be

$$\begin{array}{c}
 \text{T b c p a m} \\
 \hline
 \text{S T b c p a m}
 \end{array};
 \begin{array}{c}
 \text{T b c p a m} \\
 \hline
 \text{Cy l C p cn}_2
 \end{array};
 \begin{array}{c}
 \text{S T b c p a m} \\
 \hline
 \text{Cy l C cn}_2
 \end{array};
 \begin{array}{c}
 \text{Cy l C p cn}_2 \\
 \hline
 \text{Cy l p C cn}_2
 \end{array}$$

Among these  $F_{n+1}$  flies the combination  $\begin{array}{c} \text{T b c p a m} \\ \hline \text{Cy l C p cn}_2 \end{array}$  represents those flies which carry the test chromosome from the experimental flies, and the chromosome carrying the gene curly (Cy) from the other parent. These flies are recognised by their curly wings, non-star eyes, and purple or cinnabar eyes. These flies are then mated *inter se* to give the  $F_{n+2}$  generation (see figure 12).

Figure 12

*The Production of the  $F_{n+2}$  Generation*

$$\begin{array}{c}
 F_{n+1} \\
 \hline
 \text{Cy} \quad \text{T} \quad \text{b c p} \quad \text{a m} \\
 \quad \quad \text{l} \quad \text{C p} \quad \text{cn}_2
 \end{array}
 \times
 \begin{array}{c}
 F_{n+1} \\
 \hline
 \text{Cy} \quad \text{T} \quad \text{b c p} \quad \text{a m} \\
 \quad \quad \text{l} \quad \text{C p} \quad \text{cn}_2
 \end{array}$$

the gametes will be

$$\begin{array}{c}
 \text{T b c p a m} \\
 \hline
 \text{Cy l C cn}_2
 \end{array}
 \text{ and }
 \begin{array}{c}
 \text{T b c p a m} \\
 \hline
 \text{Cy l C p cn}_2
 \end{array}$$

the  $F_{n+2}$  combinations will be

$$\begin{array}{c}
 \text{T b c p a m} \\
 \hline
 \text{T b c p a m}
 \end{array};
 \begin{array}{c}
 \text{T b c p a m} \\
 \hline
 \text{Cy l C p cn}_2
 \end{array};
 \begin{array}{c}
 \text{T b c p a m} \\
 \hline
 \text{Cy l C p cn}_2
 \end{array};
 \begin{array}{c}
 \text{Cy l C p cn}_2 \\
 \hline
 \text{Cy l C p cn}_2
 \end{array}$$

The multiple recessives in diagram 12 are the  $\begin{array}{c} \text{T b c p a m} \\ \hline \text{T b c p a m} \end{array}$  combinations. As these are homozygous for all of their recessive genes, if any new

mutant gene has been formed on the chromosomes concerned by the action of the rays during the course of the experiment they will appear phenotypically, or, if the new gene is lethal, no multiple recessive flies will be obtained.

## APPENDIX 8

### A SYNOPSIS OF, AND REFERENCE TO, THE EARLIER EXPERIMENTS DEMONSTRATING THE OCCURRENCE OF NATURAL SELECTION.

1. *Kane* (1896) claims to have shown selection of the melanic form of *Camptogramma bilineata*.
2. *Jameson* (1898), after examination of mice on an island in Dublin Bay, reported that the hawks and owls on the island exert a preferential selection on the darker coloured mice, so that the lighter coloured ones, which more nearly approximate to the colour of the sandy background, are left in excess in the population.
3. *Weldon* (1899) attempted to demonstrate the selection of those shore crabs (*Carcinus maenas*) in Plymouth Sound with narrower frontal width of the carapace, due to the elimination of those with wider frontal width of carapace caused by accumulation of silt in the sound. This work has been strongly criticised by *Cunningham* (1928) and others.
4. *Bumpus* (1899) found that English sparrows in America with certain structural characters were selected by high winds; those with other characteristics were eliminated. *Harris* (1911) examined *Bumpus's* work statistically and agreed with his conclusions.
5. *Poulton and Saunders* (1899) exposed the pupae of *Vanessa urticae* on different contrasting backgrounds and found selective elimination by insectivorous birds.
6. *Davenport* (1908) claimed to have found a differential elimination of black and white chickens by crows among flocks consisting of black, white and pencilled birds.
7. *Thompson, Bell and Pearson* (1911) found selection round a type in the common wasp (*Vespa vulgaris*).
8. *Lutz* (1915) attempted to estimate the survival value of some structural characters of *Drosophila* by starving the insects during their embryonic development.





## BIBLIOGRAPHY

Full reference to books or papers mentioned in the text will be found in this bibliography. To find any particular reference refer to the date in the footnote at the bottom of the appropriate page in the text, or given in brackets after a name in the text. Then look in the bibliography under the name of the author concerned with the year corresponding to that of the footnote. A full list of scientific periodicals, etc., is first given with the abbreviations used in the bibliography. These are, as far as possible, the standard abbreviations given in the World List of Publications.

### LIST OF PERIODICALS AND JOURNALS IN THE BIBLIOGRAPHY WITH THEIR ABBREVIATIONS.

- Actualité scientifique.* Actualité sci.  
*Allgemeine Zeitschrift für Entomologie.* Allg. Z. Ent.  
*American Journal of Botany.* Amer. J. Bot.  
*American Journal of Science.* Amer. J. Sci.  
*American Naturalist.* Amer. Nat.  
*Anatomical Record.* Anat. Rec.  
*Anatomische Anzeiger.* Jena. Anat. Anz.  
*Annales du Muséum national d'Histoire naturelle.* Ann. du Mus.  
*Annals of the R. Botanic Gardens of Peradeniya, Ceylon.* Ann. R. Bot. Gdns. Peradeniya  
*Annals of Botany.* Ann. Bot.  
*Annals and Magazine of Natural History.* Ann. Mag. Nat. Hist.  
*Archiv für die Botanik.* Leipzig. Arch. f. Bot.  
*Archiv für Entwicklungsmechanik der Organismen (W. Roux).* Arch. Entwmech. Org.  
*Archiv für mikroskopische Anatomie (und Entwicklungsmechanik).* Bonn. Arch. mikr. Anat.  
*Archiv für Naturgeschichte.* Arch. Naturgesch.  
*Archiv für Protistenkunde.* Jena. Arch. f. Protist.  
*Archiv für Rassen und Gesellschaftsbiologie einschl.—v. Gesellschaftshygiene.* Arch. Rass.—v. GesBiol.  
*Archives de Biologie, Paris.* Arch. Biol.  
*Archives des Sciences physiques et naturelles.* Geneva. Arch. Sci. nat. et phys. Geneva.  
*Auslands—Nachrichten.* Austechnischen Zeitschriften d. Auslands. Auslands—Nachr.  
*Bericht der Deutschen Botanischen Gesellschaft.* Ber. Deutsch. Bot. Ges.  
*Bibliographia Genetica.* Bibliogr. Genet.  
*Bibliographie scientifique, bulletin de l'Institut internationale de bibliographie scientifique.* Paris. Bibliogr. sci.  
*Biographia Scientifiques.* Paris. Biograph. Sci.  
*Bijdragen tot de dierkunde.* Leiden. Bijdr. Dierk.  
*Biological Bulletin.* Biol. Bull.  
*Biological Bulletin of the Marine Biological Laboratory, Wood's Hole, Mass.* Biol. Bull. Wood's Hole.  
*Biological Reviews and Biological Proceedings of the Cambridge Philosophical Society.* Biol. Rev.  
*Biologisches Zentralblatt.* Leipzig. Biol. Zbl.  
*Biology, London.* Biology, London.  
*Biology, Health and Sociology.* Biol. Health and Sociol.  
*Biometrika.* Biometrika.  
*Biologicheskij Zhurnal.* Moscow. Biol. Zhur.

- Bolletino tecnico della coltivazione dei tabachi. R. Istituto sperimentale di Scalfati (Salerno)*  
*Portici. Boll. Tec. Tab.*  
*Botanical Gazette. Bot. Gaz.*  
*Botanical Review. Bot. Rev.*  
*British Journal of Psychology. Brit. J. Psych.*  
*Bulletin of the Academy of Sciences. St. Petersburg. Bull. Acad. Sci. St. Petersburg, and*  
*of USSR.*  
*Bulletin of Applied Botany (Plant Breeding) St. Petersburg and of U.S.S.R. Bull. Appl.*  
*Bot. (Plant Breeding).*  
*Bulletin International de l'Academie des Sciences de Cracovie (de l'Academie polonaise des*  
*Sciences). Bull. int. Acad. Cracovic.*  
*Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew), London. Kew Bull.*  
*Bulletin of the Peabody Museum of Natural History. Bull. Peabody Mus.*  
*Bulletin of the United States National Museum, Smithsonian Institute, Washington.*  
*Bull. U.S. Nat. Mus.*  
*Bulletin de la Société d'études des Sciences naturelles de l'ouest de la France. Bull. Soc. Sci.*  
*Nat. Ouest de la France.*  
*California Citrograph. Calif. Citrogr.*  
*Cambridge Philosophical Society. Camb. Phil. Soc.*  
*Carnegie Institute of Washington Publications. Carn. Inst. Wash. Pubs.*  
*Carnegie Institute of Washington, Year Book. Carn. Inst. Wash. Year Book.*  
*Catholic Herald. Cath. Her.*  
*Compte rendu de l'Academie des Sciences de l'U.R.S.S. C.R. Acad. Sci. U.R.S.S.*  
*Compte rendu hebdomadaire des Sciences de l'Academie des Sciences. Paris. C.R. Acad.*  
*Sci. Paris.*  
*Compte rendu hebdomadaire des séances et memoires de la Société de Biologie. Paris. C.R.*  
*Soc. Biol. Paris.*  
*Compte rendu des travaux du Laboratoire de Carlsberg. C.R. Lab. Carlsberg.*  
*Contemporary Review. Contemp. Rev.*  
*Cytologia, Fuji. Cytologia.*  
*Cytologia, Fuji. Jubilee volume. Cytologia. Jub. Vol.*  
*Ecology. Ecology.*  
*The Entomologist. Entomologist.*  
*Ergebnisse der Anatomie u. Entwicklungsgeschichte. Ergeb. Anat. Ent. Gesch.*  
*Ergebnisse der Biologie. Ergeb. Biol.*  
*Flora. Flora.*  
*Forestry. Forestry.*  
*Genetica. s'Gravenhage. Genetica.*  
*Genetics. Genetics.*  
*Geognostische Jahresthefte. München. Geog. Jh.*  
*Handbuch der Vererbungswissenschaft. Handb. Vererbungsw.*  
*Hereditas genetiskt arkiv. Hereditas.*  
*Hilgardia. Hilgardia.*  
*Internationale entomologische Zeitschrift. Int. ent. Z.*  
*Irish Naturalist. Irish Nat.*  
*International Congress for Arts and Sciences. New York and London. Int. Congr.*  
*Arts and Scis.*  
*Internationale Revue der gesamten Hydrobiologie u. Hydrographie. Int. Rev. Hydrobiol.*  
*Japanese Journal of Botany. Tokyo. Jap. J. Bot.*  
*Jenaische Zeitschrift für Naturwissenschaft. Jena. Z. Naturw.*  
*Journal of Agricultural Research. J. Agric. Res.*

- Journal of the College of Science. Imperial University of Tokyo.* J. Coll. Sci. Tokyo.  
*Journal of Ecology.* J. Ecol.  
*Journal of Economic Entomology.* J. Econ. Ent.  
*Journal of Experimental Biology.* J. Exp. Biol.  
*Journal of Botany, British and Foreign.* London. J. Bot. London.  
*Journal of Experimental Zoology.* J. Exp. Zool.  
*Journal of Genetics.* J. Genet.  
*Journal of Heredity.* J. Hered.  
*Journal of Infectious Diseases.* J. infect. Dis.  
*Journal of the Linnean Society (Zoology) London.* J. Linn. Soc. (Zool).  
*Journal of the Marine Biological Association.* J. Mar. Biol. Assoc.  
*Journal of Morphology (and Physiology).* J. Morph.  
*Journal of Pathology and Bacteriology.* London. J. Path. Bact.  
*Journal Science, Hiroshima University.* J. Sci. Hiroshima Univ.  
*Klinische Monatsblätter für Augenheilkunde.* Klin. Mbl. Augenheilk.  
*Kosmos.* Kosmos.  
*Lloydia.* Lloydia.  
*Medecinische Jahrbucher des K.K. Osterreichischen Staates.* Osterreichische. Medecinische Jahrbucher.  
*Memoirs of the Boston Society of Natural History.* Mem. Boston Soc. Nat. Hist.  
*Memoirs de la Soci  t   de physique et d'Histoire naturelle de G  n  ve.* Mem. Soc. Phys. et d'Hist. Nat. Genev.  
*Morphologische Jahrbuch.* Leipzig. Morph. Jb.  
*Nachrichten von der Gesellschaft der Wissenschaften zu G  ttingen.* Nachr. Ges. Wiss. G  ttingen.  
*Natural Science.* Nat. Sci.  
*Nature, London.* Nature. Lond.  
*Naturwissenschaften.* Naturwissenschaft.  
*Naturwissenschaftliche Wochenschrift.* Naturw. Wschr.  
*Neue Denkschriften der Allgemein Schweizerischen Gesellschaft f  r die gesamten Naturwissenschaften.* Zurich. N. Denkschr. Schweiz. Ges. Naturws.  
*New Phytologist.* New Phytol.  
*Nineteenth Century.* Nineteenth Cent.  
*North British Review.* North. Brit. Rev.  
*Philosophical Transactions of the Royal Society of London, B.* Phil. Trans. R. Soc. London. B.  
*Physiological Reviews.* Physiol. Rev.  
*Planta.* Planta.  
*Proceedings of the American Academy of Arts and Sciences.* Boston. Proc. Amer. Acad. Arts and Sci.  
*Proceedings of the American Philosophical Society.* Proc. Amer. Phil. Soc.  
*Proceedings of the 6th International Congress of Genetics.* Ithaca. Proc. 6th Int. Congr. Gen.  
*Proceedings of the National Academy of Sciences.* Washington. Proc. Nat. Acad. Sci. Wash.  
*Proceedings of the Philadelphia Academy of Natural Sciences.* Proc. Phila. Acad. Nat. Sci.  
*Proceedings of the Royal Society of Edinburgh.* Proc. Roy. Soc. Edin.  
*Proceedings of the Royal Society of London. B.* Proc. Roy. Soc. Lond. B.  
*Proceedings of the Society for Experimental Biology and Medicine.* New York. Proc. Soc. exp. Biol.  
*Proceedings of the University of Durham Philosophical Society.* Proc. Univ. Durham Phil. Soc.  
*Protoplasma.* Leipzig. Protoplasma.

*Quarterly Review of Biology.* Quat. Rev. Biol.

*Report of the British Association for the Advancement of Science.* London. Rep. Brit. Assoc.

*Science.* Science.

*Science Monthly.* Sci. Monthly.

*Science Progress.* Sci. Progr.

*Scientia.* Scientia.

*Scientific Agriculture.* Ottawa. Sci. Agric.

*Sitzungsberichte der Kgl. Preussischen Akademie der Wissenschaften Berlin.* Maths.—

Phys. Kl. S.B. Preuss. Akad. Wiss.

*Sitzungsberichte der Mathematisch-naturwissenschaftlichen abteilung der bayerischen Akademie der Wissenschaften zu München.* S.B. bayer. Akad. Wiss.

*Smithsonian Miscellaneous Collections.* Smithsonian Misc. Coll.

*Transactions of the American Philosophical Society.* Trans. Amer. Phil. Soc.

*Transactions of the Royal Entomological Society of London.* Trans. Roy. Ent. Soc. London.

*Transactions of the New York Academy of Science.* Trans. New York Acad. Sci.

*Transactions of the Victoria Institute.* London. Trans. Vic. Inst. London.

*University of California Publications in Agricultural Sciences.* Berkeley. Univ. Calif. Publ. Agric. Sci.

*University of California Publications in Botany.* Berkeley. Univ. Calif. Publ. Bot.

*Vasculum.* Newcastle. Vasculum.

*Verhandlungen des V. Internationalen Kongresses für Vererbungswissenschaft Berlin.*

Verh. d. V. Int. Kongr. f. Vererb. Berlin.

*Verhandlungen der K.K. Zoologisch-botanischen Gesellschaft in Wien.* Verh. Zool-bot. Ges. Wien.

*Verhandlungen des Naturforschenden Vereine in Brünn.* Verh. naturf. Ver. Brünn

*Verhandlungen der Physikalisch-medizinischen Gesellschaft zu Würzburg.* Verh. Phys.-med. Ges. Würzburg.

*Verhandlungen der Schweizerischen Naturforschenden Gesellschaft.* Verh. Schweiz. naturf. Ges.

*Vorträge u. Aufsätze über Entwicklungsmechanik der Organismen.* Vortr. EntwMech. Org.

*Zeitschrift für Biologie.* Z. Biol.

*Zeitschrift für induktiv Abstammungs—u. Vererbungslehre.* Zeits. indukt. Abstamm.—u. VererbLehre.

*Zeitschrift für induktiv Abstammungs—u. Vererbungslehre.* Supplement. Zeits. indukt. Abstamm. u. VererbLehre. Suppl.

*Zeitschrift für wissenschaftliche Zoologie.* Z. wiss. Zool.

*Zeitschrift für Zellforschung und Mikroskopische Anatomie.* Z. Zellforsch.

*Zoologischer Anzeiger.* Zool. Anz.

*Züchter Zeitschrift für theoretische und angewandte Genetik.* Berlin. Züchter.

## PUBLICATIONS

- Ackert, J. E., 1916. On the Effects of Selection in *Paramecium*. *Genetics*, 1, 387.
- Agar, W. E., 1913. Transmission of Environmental Effects from Parent to Offspring in *Simonecephalus velutus*. *Proc. Roy. Soc. Lond. B.*, 203, 319.
- Agar, W. E., 1935. A First Report on a test on McDougall's Lamarckian Experiment on the Training of Rats. *J. Exp. Biol.*, 8, 95.
- Agassiz, L., and Gould, A. A., 1851. *Principles of Zoology*. Boston.
- Agol, I. J., 1931. Step Allelomorphism in *Drosophila melanogaster*. *Genetics*, 16, 254.
- Altenburg, E., 1928. The Limit of Radiation Frequency Effective in Producing Mutations. *Amer. Nat.*, 62, 540.
- Altenburg, E., 1933. The Production of Mutations by Ultra-violet Light. *Science*, 78, 587.
- Altenburg, E., 1934. The Artificial Production of Mutations by Ultra-violet Light. *Amer. Nat.*, 68, 491.
- Anderson, E., 1937. Supra-specific Variations in Nature and in Classification. *Amer. Nat.*, 71, 223.
- Anderson, I., 1927. Notes on some Characters in Ferns subject to Mendelian Inheritance. *Hereditas*, 9, 157.
- Aquinas, St. Thomas. *Summa Contra Gentiles*. London. Translated by Fathers of the English Dominican Province, 1912.
- Aquinas, St. Thomas. *Summa Theologica*. London. Translated by Fathers of the English Dominican Province, 1912.
- Aristotle. *The Works of Aristotle Translated into English*. Under the general editorship of J. A. Smith and W. D. Ross, Oxford. Individual parts are as follows:
- Vol. 2. *Physica*, 1930. R. P. Hardie and R. K. Gaye.
- De Caelo*, 1922. J. L. Stocks.
- De Generatione et Corruptione*, 1922. H. H. Joachim.
- Vol. 3. *De Anima*, 1931. J. A. Smith.
- Vol. 4. *Historia Animalium*, 1910. D'Arcy Wentworth Thompson.
- Vol. 5. *De Partibus Animalium*, 1912. W. Ogle.
- De Generatione Animalium*. 1912. A. Platt.
- Armstrong, H. E., 1936. Insect Coloration. *Nature*, Lond., 138, 242.
- Astauroff, B. L., 1933. The Experimental Production of Mutations in the Silkworm. (*Bombyx mori* L.). *Z. Biol.*, 2, 116, in Russian.
- Babcock, E. B., and Clausen, R. E., 1927. *Genetics in Relation to Agriculture*. 2nd ed. New York.
- Babcock, E. B., and Collins, J. L., 1929. Does Natural Ionizing Radiation control the Rate of Mutation? *Proc. Nat. Acad. Sci. Wash.*, 15, 623.
- Babcock, E. B., and Navaschin, M., 1930. The Genus *Crepis*. *Bibliogr. Genet.* 6, 1.
- Baily, J. R., Jr., 1941. A Contribution to the Theory of Evolution by Natural Selection. *Amer. Nat.*, 75, 213.
- Baird, J. L., 1873. *The Darwinian Theory and the Law of the Migration of Organisms*. Trans. from Wagner, London.
- Baldwin, J. Mark, 1896. A New Factor in Evolution. *Amer. Nat.*, 30.
- Baldwin, J. M., 1902. *Development and Evolution*.
- Banta, A. M., 1921. Selection in *Cladocera*. *Carn. Inst. Wash. Pubs.*, 305, 1.
- Banta, A. M., and Wood, T. R., 1927. A Thermal Race of *Cladocera* Originating by Mutation. *Verh. d. V. Int. Kongr. f. Vererb. Berlin*, 1, 397.
- Banta, A. M., and Wood, T. R., 1939. Genetic Studies in Sexual Reproduction. *Carn. Inst. Wash. Pubs.*, 513, 131.

- Bartolucci, A., 1939. Il fenomeno della poliploidia ed il Tabacco. *Boll. Tec. Tab.*, 36, 141.
- Basil, St., Hexaem Horn.
- Bateson, W., 1894. *Materials for the Study of Variation*. London.
- Bateson, W., and Punnett, R. C., 1905. A Suggestion as to the Nature of the Walnut Comb in Fowls. *Camb. Phil. Soc.*, 13, 165.
- Bateson, W., 1909. *Mendel's Principles of Heredity*. Cambridge.
- Baur, E., 1924. Untersuchungen über das Wesen die Entstehung und die Vererbung von Rassen unterscheiden bei *Antirrhinum majus*. *Bibliogr. Genet.*, 4, 1.
- Baur, E., 1925. Die Bedeutung der Mutationen für das Evolutionsproblem. *Zeits. indukt. Abstamm.—u. Vererb. Lehre*, 37, 107.
- Belgowsky, M. L., 1937. A comparison of the frequency of induced mutations in *Drosophila simulans* and in its hybrid with *D. melanogaster*. *Genetics*, 19, 370.
- Belgowsky, M. L., and Muller, H. J., 1938. Further Evidence of the prevalence of minute re-arrangements and absence of simple breakage in and near to chromocentral regions, and its bearing on the mechanisms of Mosaicism and re-arrangements. *Genetics*, 23, 139.
- Beljajeff, M. M., 1927. Ein Experiment über die Bedeutung der Schutzzüchtung. *Biol. Zbl.*, 47, 107.
- Belling, J., 1925. Homologous and similar Chromosomes in diploid and triploid *Hyacinthus*. *Genetics*, 10, 59.
- Belt, Thomas, 1874. *The Naturalist in Nicaragua*.
- Beneden, E. van., 1884. Recherches sur la Mutation de l'oeuf, la fécondation et la division cellulaire. *Arch. Biol. Paris*.
- Benn, A. W., 1914. *The Greek Philosophers*. 2nd ed., London.
- Bentham, G., and Hooker, J. D., 1883. *Genera Plantarum*. London.
- Berg, L. S., 1926. *Nomogenesis, or Evolution determined by Law*. Trans. by J. N. Rostovtsov. London.
- Bergner, A. D., and Blakeslee, A. F., 1932. Cytology of the *ferax-stramonium* triangle in *Datura*. *Proc. Nat. Acad. Sci. Wash.*, 18, 151.
- Bergner, A. D., Satina, S., and Blakeslee, A. F., 1933. Prime Types in *Datura*. *Proc. Nat. Acad. Wash.*, 19, 103.
- Bernard, J. H. See Kant.
- Blackburn, K. B., and Harrison, J. W. H., 1924. Genetical and Cytological Studies in Hybrid Races. 1. The Origin of a fertile hexaploid Form in the *Pimpinellifolia-Villosa* crosses. *J. Exp. Biol.*, 1, 557.
- Blainville, Ducratay de, 1890. Cuvier et Geoffroy Saint-Hilaire. *Biograph. Sci. Paris*.
- Blakeslee, A. F., 1922. Variations in *Datura* due to Changes in chromosome Number. *Amer. Nat.*, 56, 16.
- Blakeslee, A. F., 1928. Genetics of *Datura*. *Verh. d. V. Int. Congr. f. Vererb. Berlin. Suppl.*, 1, 117.
- Blakeslee, A. F., 1929. Cryptic Types in *Datura* due to chromosomal interchange and their geographical distribution. *J. Hered.*, 20, 177.
- Blakeslee, A. F., 1930. Extra Chromosomes, a Source of Variations in the Jimson Weed. *Smithsonian Report*, 84, 431.
- Blakeslee, A. F., 1932. The Species Problem in *Datura*. *Proc. 6th Int. Congr. Gen.*, 1, 104.
- Blakeslee, A. F., and Belling, J., 1924. Chromosomal Mutations in the Jimson Weed, *Datura stramonium*. *J. Hered.*, 15, 194.
- Blakeslee, A. F., Bergner, A. D., and Avery, A. G., 1937. Geographical Distribution of Chromosome Prime Type in *Datura stramonium*. *Cytologia, Jub. vol.*, 1070.
- Blakeslee, A. F., and Collaborators, 1929. Analysis of *Datura stramonium* plants grown from seed exposed to X-rays. *Anat. Rec.*, 44, 281.
- Boettger, C. R., 1931. Die Entstehung von Populationen mit bestimmter Variantanzahl die *Capea*. *Zeits. indukt. Abstamm.—u. Vererb. Lehre*, 58, 295.

- Boveri, Th., 1902. Ueber mehrpolige Mitosen als Mittel zur Analyse des Zellkerns. *Verh. Phys.-med. Ges. Würzburg.*, 33.
- Boveri, Th. Ueber die Entwicklung dispermer Ascarisier. *Zool. Anz.*, 27.
- Brecker, L., 1923. Lichtbeeinflusste Schmetterlingspuppen und deren Nachkommen. *Zeits. indukt. Abstamm.-u. VererbLehre*, 30.
- Bridges, C. B., 1921. Triploid Intersexes in *Drosophila melanogaster*. *Science*, 54, 252.
- Bridges, C. B., 1922. The Origin of Variations in Sexual and Sex-limited Characters. *Amer. Nat.*, 56, 51.
- Bridges, C. B., 1935. Salivary Chromosome Maps. *J. Hered.*, 26, 60.
- Bridges, C. B., 1936. The "bar" Gene, a duplication. *Science*, 83, 210.
- Bridges, C. B., 1938. A revised Map of the Salivary Gland X Chromosome in *Drosophila*. *J. Hered.*, 29.
- Brink, R. A., 1935. Cytogenetic Evolutionary Processes and their Bearing on Evolutionary Theory. Cytogenetic Evolutionary Processes in Plants. *Amer. Nat.*, 69, 97.
- Brunfels, 1530. *Herbarium*.
- Budge, D., 1912. *Egyptian Literature*, Vol. 1. *Legends of the Gods*. London.
- Buffon, M. de., *Histoire Naturelle*. Many volumes, beginning in 1794; the last one was published posthumously in 1804. See especially volume *Histoire naturelle des Animaux*.
- Buhlholz, T. T., and Blakeslee, A. F., 1930. Radium Experiments with *Datura*. *J. Hered.*, 21, 119.
- Bumpus, H. C., 1899. The Elimination of the Unfit as illustrated by the Introduced Sparrow. *Biol. Bull. Wood's Hole*, 11, 209.
- Burnet, J., 1930. *Early Greek Philosophy*. 4th ed., London.
- Butler, Samuel, 1920. *Luck or Cunning?* 2nd ed., London.
- Butler, Samuel. *Unconscious Memory*. London.
- Butler, Samuel. *Evolution Old and New*. London.
- Butler, Samuel. *Life and Habit*. London.
- Butschli, O., 1897. *Untersuchungen über microscopische Schaume und das Protoplasma*. Leipzig.
- Buxton, B. H., and Newton, W. C. F., 1928. Hybrids of *Digitalis ambigua* and *Digitalis purpurea*, their Fertility and Cytology. *J. Genet.*, 19, 269.
- Carothers, E. E., 1913. The Mendelian ratio in certain Orthopteran Chromosomes. *J. Morph.*, 24, 487.
- Carothers, E. E., 1917. The Segregation and Recombination of Homologous Chromosomes as found in two genera of *Acrididae* (Orthoptera). *J. Morph.*, 28, 255.
- Carothers, E. E., 1921. Genetical Behaviour of Heteromorphic Homologous Chromosomes of *Circotettix* (Orthoptera). *J. Morph.*, 35, 457.
- Carothers, E. E., 1926. The Mutation Divisions in relation to the Segregation of Homologous Chromosomes. *Quat. Rev. Biol.*, 1, 419.
- Carpenter, G. D. H., 1936. Insect Coloration. *Nature*, Lond., 138, 243.
- Carpenter, G. D. H., 1936. Insect Coloration and Natural Selection. *Nature*, Lond., 138, 686.
- Carpenter, G. D. H., 1936. Natural Selection. *Nature*, Lond., 138, 1017.
- Carpenter, G. D. H., 1936-37. The Factors of Mimicry still require Natural Selection for their Explanation. *Proc. Roy. Soc. Lond. B.*, 121, 65.
- Carr, H. W., 1929. *Leibniz*. London.
- Carrick, R., 1936. Experiments to Test the Efficiency of Protective Adaptations in Insects. *Trans. R. Ent. Soc. Lond.*, 85, 131.
- Carus, V., 1872. *Geschichte der Zoologie*. Leipzig.
- Catchpool, E., 1884. An Unnoticed Factor in Evolution. *Nature*, Lond., 31, 4.
- Catholic Encyclopedia, 1909. Edited by Herbermann and others. 15 vols. London.



- Cesalpino, 1583. *De Plantis*.
- Cesnola, A. P. di, 1904. Preliminary Note on the Protective Value of Colour in *Manitis Religiosa*. *Biometrika*, 3, 58.
- Chalmers, R. E., 1930. Mutations and Freaks from x-rayed Malcs of *Habrobracon*. *Anat. Rec.*, 47, 394.
- Chambers, R., *Vestiges of the Natural History of Creation*. 11th ed. London.
- Chen, Tuan, 1929. Twenty-five Centuries before Charles Darwin. *Sci. Monthly*, 29, 49.
- Child, G., 1935. Phenogenetic Studies on Scute-1 of *D. melanogaster*. *Genetics*, 20.
- Clausen, J., 1927. Chromosome Number and the Relationship of Species in the Genus *Viola*. *Ann. Bot.*, 43, 741.
- Clausen, J. Cytogenetic and Taxonomic Investigations in *Melanium* Violets. *Hereditas*, 15, 219.
- Clausen, J., 1933. Cytological Evidence for the Hybrid Origin of *Pentstemon neotericus* Keck. *Hereditas*, 18, 65.
- Clausen, J., Keck, D. D., and Hiesey, W. M. Experimental Taxonomy. *Carn. Inst. Wash. Year Book*, No. 37, 218.
- Clausen, J., Keck, D. D., and Hiesey, W. M., 1940. Experimental Studies on the Nature of Species. 1. Effects of Varied Environments on Western North American Plants. *Carn. Inst. Wash. Pubs.*, 520, 1.
- Clausen, R. E., and Goodspeed, T. H., 1925. Interspecific Hybridization in *Nicotiana* 11. A tetraploid *Glutinosatabacum* Hybrid. An Experimental Verification of Winge's Hypothesis. *Genetics*, 10, 279.
- Cleland, R. E., 1931. Cytological Evidence of Genetical Relationships in *Oenothera*. *Amer. J. Bot.*, 18, 629.
- Cleland, R. E., and Blakeslee, A. F., 1930. Interaction between Complexes for Segmental Interchanges in *Oenothera*. *Proc. Nat. Acad. Sci. Wash.*, 16, 183.
- Clodd, E., 1907. *Pioneers of Evolution*. Rev. ed. London.
- Cole, F. J., 1944. *A History of Comparative Anatomy*. London.
- Collingwood, R. G., 1945. *The Idea of Nature*. Oxford.
- Collins, J. L., 1927. A Low Temperature Type of Albinism in Barley. *J. Hered.*, 18, 331.
- Collins, J. L., Hollingshead, L., and Avery, P. 1929. Interspecific Hybrids in *Crepis* III. Constant Fertile Forms containing Chromosomes derived from two Species. *Genetics*, 14, 305.
- Cooper, D. C., and Brink, R. A. Cytological Evidence for Segmental Interchange between Non-homologous Chromosomes in Maize. *Proc. Nat. Acad. Sci. Wash.*, 17, 334.
- Cope, E. D., 1869 and 1886. *The Origin of Genera*. *Proc. Phila. Acad. Nat. Sci.*, and published as a chapter in the *Origin of the Fittest*, 1887.
- Cope, E. D., 1899. *The Primary Factors of Organic Evolution*.
- Cope, E. D., 1887. *The Origin of the Fittest*. New York.
- Correns, C., 1907. *Bestimmung und Vererbung des Geschlechtes*. Leipzig.
- Cott, H. B., 1940. *Adaptive Coloration in Animals*. London.
- Coulter, J. M., 1926. The History of Organic Evolution. *Science*, 53, 487.
- Crampton, H. E., 1904. Experimental and Statistical Studies upon *Lepidoptera*. 1. Variation and Elimination in *Philosamia cynthia*. *Biometrika*, 3, 113.
- Creighton, H. B., and McClintock, B., 1931. A Correlation of Cytological and Genetical Crossing-over in *Zea mays*. *Proc. Nat. Acad. Sci. Wash.*, 17, 492.
- Crew, F. A. E., 1927. The Germplasm and its Architecture. *Nature*, Lond., 120, 732.
- Crew, F. A. E., 1930. *Eugenics Review*, 1930.
- Crew, F. A. E., 1936. A Repetition of McDougall's Lamarckian Experiment. *J. Genet.*, 33, 61.
- Cunningham, J. T., and MacMunn, C. A., 1893. On the Coloration of the Skins of Fishes, especially of *Pleuronectidae*. *Phil. Trans. Roy. Soc. London, B.*, 184, 765.

- Cunningham, J. T., 1895-97. Additional Evidence on the Influence of Light in producing Pigment on the Lower Sides of Flat-fishes. *J. Mar. Biol. Assoc.*, 4, N.S.
- Cunningham, J. T., 1928. *Modern Biology*. London.
- Cuvier, Baron, 1798. *Tableau élémentaire de l'Histoire naturelle des Animaux*. Paris.
- Cuvier, Baron, 1816-17. *Le Règne Animal, distribué d'après son Organisation*. Paris.
- Cuvier, Baron, 1834. *Le Règne Animal*. English trans. by H. McMurtie. London.
- Cuvier, Baron, 1834. *Le Règne Animal*. English Trans. Anon., containing a memoir of Cuvier.
- Dampier, Whelham, 1930. *A History of Science*. Cambridge. 2nd Ed.
- Danilevsky, N. J., 1885. *Darwinism: A Critical Study*. Vol. 1.
- Darlington, C. D., 1936. Crossing-over and its Mechanical Relationships in *Chorthippus* and *Stauroderus*. *J. Genet.*, 33, 465.
- Darlington, C. D., 1937. *Recent Advances in Cytology*. London. 2nd Ed.
- Darlington, C. D., and Gairdner, A. E., 1937. The Variation System in *Campanula persicifolia*. *J. Genet.*, 35, 97.
- Darwin, C., 1859. *On the Origin of Species by Means of Natural Selection and the Preservation of Favoured Races in the Struggle for Life*. 3rd Ed. used here mostly.
- Darwin, C., 1868. *Variations of Plants and Animals under Domestication*.
- Darwin, C., 1871. *The Descent of Man and Selection in Relation to Sex*.
- Darwin, E., 1791. *The Botanic Garden*.
- Darwin, E., 1794-96. *Zoonomia: or the Laws of Organic Life*.
- Darwin, E., 1803. *The Temple of Nature: or the Origin of Society*.
- Darwin, F., 1887. *The Life and Letters of Charles Darwin*. 3 Vols. London.
- Darwin, F., 1892. *Life of Charles Darwin*. London.
- Darwin, F., 1903. *More Letters of Charles Darwin*. 2 Vols. London.
- Darwin, F., and Seward, A. C., 1903. In *More Letters of C. Darwin*, by F. Darwin, 1903.
- Daudin, H., 1926. *Les Classes Zoologiques et l'Idée de Série Animaux*. 2 Vols. Paris.
- Davenport, C., 1908. Elimination in Self-coloured Birds. *Nature*, London, 78, 101.
- Davies, J. R. Ainsworth, 1903. *The Natural History of Animals*. 4 Vols (in 8 Books). London.
- Davies, J. R. Ainsworth, 1907. *Thomas H. Huxley*. English Men of Science Series. London.
- Davies, L. Merson, 1935. In Discussion on the Supposed Links Between Man and the Lower Animals. *Trans. Vic. Inst.*, 67, 179.
- Delage, Yves, 1903. *La Structure du Protoplasma et les Théories sur l'Hérédité*. 2nd ed. Paris.
- Delage, Yves, and Goldsmith, M., 1912. *The Theories of Organic Evolution*. London.
- Delaunay, L. N., 1926. Phylogenetische Chromosomenverkürzung. *Z. Zellforsch.*, 4, 338.
- Delaunay, L. N., 1929. Kern und Art. Typische Chromosomenformen. *Planta*, 7, 100.
- Delaunay, L. N., 1930. Die Chromosomen aberranten in der Nachkommenschaft von röntgenisierten Ahnen einer reimen Linie von *Triticum vulgare albidum*. *Zeits. induct. Abstamm. u. VererbLehre*, 55, 352.
- Dembowski, J., 1926. Zur Kritik der Faktoren und Chromosomenlehre. *Zeits. induct. Abstamm.—u. VererbLehre.*, 51, 216.
- Demerec, M., 1926. Miniature-alpha—a second frequently mutating Character in *Drosophila virilis*. *Proc. Nat. Acad. Sci. Wash.*, 12, 687.
- Demerec, M., 1927. Magenta-alpha—a third frequently mutating Character in *Drosophila virilis*. *Proc. Nat. Acad. Sci. Wash.*, 13, 249.
- Demerec, M., 1928. The Behaviour of Mutable Genes. *Zeits. induct. Abstamm.—u. VererbLehre*. 53, 234, Suppl.
- Demerec, M., 1928b. Mutable Characters of *Drosophila virilis*. 1. Reddish-alpha Body-character. *Genetics*, 13, 359.

- Demerec, M., 1929. Genetic Factors stimulating Mutability of the Miniature-gamma Wing Character of *Drosophila virilis*. *Proc. Nat. Acad. Sci. Wash.*, 15, 834.
- Demerec, M., 1930. Changes in the Rate of Mutability of the Mutable Miniature Gene of *Drosophila virilis*. In memorial volume to Prof. Ruzicka, Prague.
- Demerec, M., 1932. Changes in the Instability of Miniature-3 Gene of *Drosophila* during ontogeny. *Proc. 6th int. Congr. Gen.*, 2, 43.
- Demerec, M., 1932b. Rate of Instability of Miniature-3 Gene of *Drosophila virilis* in the Males, in the homozygous and in the heterozygous Females. *Proc. Nat. Acad. Sci. Wash.*, 18, 656.
- Demerec, M., 1934. The Effect of X-rays on the Rate of Change in the Unstable Miniature-3 Gene of *Drosophila virilis*. *Proc. Nat. Acad. Sci. Wash.*, 20, 28.
- Demerec, M., 1935. The Role of Genes in Evolution. *Amer. Nat.*, 69, 125.
- Demerec, M., 1936. Frequency of "cell-lethals" among Lethals obtained at random in the X-chromosome of *Drosophila melanogaster*. *Proc. Nat. Acad. Sci. Wash.*, 22, 350.
- Demerec, M., 1937. The Frequency of Spontaneous Mutations in Certain Stocks of *Drosophila melanogaster*. *Genetics*, 22, 469.
- Dermen, H., 1940. Colchicine Polyploidy and Technique. *Bot. Rev.*, 6, 599.
- Dewar, D., 1931. *Difficulties of the Evolution Theory*. London.
- Dewar, D., 1938. *More Difficulties of the Evolution Theory*. London.
- Dewar, D., 1940. *Man: A Special Creation*. London.
- Dewar, D., 1941. Evolution: Rejected by Many. *Cath. Her.* London, March 14th.
- Dewar, D., 1941b. The Case Against Evolution. *Cath. Her.* London, April 4th.
- Dewar, D., 1941c. Evolution: Rejection of Evidence. *Cath. Her.* London, May 16th.
- Dewar, D., 1941d. Evolution. *Cath. Her.* London, June 29th.
- Dickson, H., 1932. The Effects of X-rays, Ultra-violet Light and Heat in Producing Saltants in *Chaetomium Cochliodes* and other Fungi. *Ann. Bot.*, 46, 389.
- Dickson, H., 1933. Saltation induced by X-rays in seven Species of *Chaetomium*. *Ann. Bot.*, 47, 735.
- Dickson, R. C., 1940. Inheritance of Resistance to Hydrocyanic Acid Fumigation in the California Red Scale. *Hilgardia*, 7.
- Diels, H., 1879. *Doxographi Graeci*. Berlin.
- Digby, L., 1912. The Cytology of *Primula Kewensis* and of other related *Primula* Hybrids. *Ann. Bot.*, 26, 357.
- Diver, C., 1936-37. The Problem of Closely Related Species and Distribution of their Populations. *Proc. Roy. Soc. London, B*, 121, 62.
- Dobell, C., 1925. The Chromosome Cycle of the *Sporozoa* Considered in Relation to the Chromosome Theory of Heredity. *La Cellule*, 35, 169.
- Dobrovol'skaia-Zavadaia, N. A., 1927. Etude sur les Effets Produits par les Rayons X dans le Testicule chez les Souris. *Arch. mikr. Anat.*, 33, 396.
- Dobrovol'skaia-Zavadaia, M. A., 1928. L'Irradiation des Testicules et l'Hérédité chez les Souris. *Arch. Biol.*, 38, 457.
- Dobzhansky, T., 1927. Studies on the Manifest Effects of Certain Genes in *Drosophila melanogaster*. *Zeits. indukt. Abstamm.*—u. VererbLehre, 43, 330.
- Dobzhansky, T., 1935. Fecundity in *Drosophila pseudo-obscura* at Different Temperatures. *J. Exp. Zool.*, 71, 449.
- Dobzhansky, T., 1935b. The Y-Chromosome of *Drosophila pseudo-obscura*. *Genetics*, 20, 366.
- Dobzhansky, T., 1935c. *Drosophila miranda*, a new Species. *Genetics*, 20, 377.
- Dobzhansky, T., 1937. Further Data on the Variation of the Y-Chromosome in *Drosophila pseudo-obscura*. *Genetics*, 22, 340.
- Dobzhansky, T., 1941. *Genetics and the Origin of Species*. Columbia Univ., 2nd ed.

- Dobzhansky, T., and Socolow, D., 1939. Structure and Variation in *Drosophila azteca*. *J. Hered.*, 30, 3.
- Dobzhansky, T., and Sturtevant, A. H., 1938. Inversion in Chromosomes of *Drosophila pseudo-obscura*. *Genetics*, 23, 28.
- Dobzhansky, T., and Tan, C. C., 1936. Studies on Hybrid Sterility 3. A Comparison of the Gene Arrangement in Two Species. *Drosophila pseudo-obscura* and *Drosophila miranda*. *Zeits. indukt. Abstamm.—u. VererbLehre*, 72, 88.
- Doncaster, L., 1908. On Sex Inheritance in the Moth *Abraxas grossulariata* and its Variety *lacticolor*. *Rep. Evolution Committee of the Roy. Soc.*, 4.
- Dorlodot, Canon, 1925. *Darwinism and Catholic Thought*. London.
- Driesch, H., 1908. *The Science and Philosophy of the Organism*. London.
- Driesch, H., 1914. *The History and Theory of Vitalism*. Trans. by C. K. Ogden, London.
- Dubinín, N. P., 1929. Alklomorphentreppen bei *Drosophila melanogaster*. *Biol. Zbl.*, 49, 328.
- Dubinín, N. P., and others, 1934. Experimental Study of the Ecogenotypes of *Drosophila melanogaster*. 1 and 2. *Biol. Zhur.*, 3, 166.
- Dubinín, N. P., 1936. Genetic Constitution and Genedynamics of *Drosophila melanogaster*. *Biol. Zhur.*, 5, 939.
- Dubinín, N. P., 1937. The Aberrative Polymorphism in *Drosophila melanogaster* (*fasciata*). *Biol. Zhur.*, 6, 311.
- Dubinín, N. P., Socolow, N. N., and Timiakoff, G. G., 1937. Intraspecific Chromosome Variability. *Biol. Zhur.*, 6, 1049.
- Dudycha, G. J., 1929. What is Evolution? *Sci. Monthly*, 29, 271.
- Dudycha, G. J., 1932. Ideas of Origin among the Ancient Egyptians and Babylonians. *Sci. Monthly*, 32, 263.
- Duerden, J. E., 1920. Inheritance of Callosities in the Ostrich. *Amer. Nat.*, 54, 289.
- Duggar, B. M., 1936. *Biological Effects of Radiation*, vol. 2. A Symposium, New York.
- Duncan, F. B., 1915. An Attempt to Produce Mutations Through Hybridization. *Amer. Nat.*, 49, 575.
- Durham, F. M., 1908. A Preliminary Account of the Inheritance of Coat-colour in Mice. *Rep. Evolution Committee of the Roy. Soc.*, 4, 41.
- Dürkhen, B., 1923. Ueber die Wirkung Farbigen Lichtes auf die Puppen des Kohlweisslings (*Pieris brassicae*) und des Verhalten der Nachkommen. *Arch. Entwemch. Org.*, 99, 222.
- East, E. M., 1934. The Nucleus-plasma Problem. *Amer. Nat.*, 68, 289 and 402.
- East, E. M., 1935. Genetic Reactions in Nicotiana. 1, 2 and 3. *Genetics*, 20, 403.
- East, E. M., 1936. Genetic Aspects of Certain Problems of Evolution. *Amer. Nat.*, 70, 143.
- Edwards, Milne, 1896. *A Manual of Zoology*. Trans. by R. Knox. London.
- Eimer, G. H. T., 1890. *Organic Evolution as the Result of the Inheritance of Acquired Characters*. Trans. by J. T. Cunningham.
- Ellenhorn, J., Prokofjeva, A., and Muller, H. J., 1935. The Optical Dissociation of *Drosophila* Chromosomes by means of Ultra-violet Light. *C. R. Acad. Sci. U.R.S.S.*, 1, 234.
- Elliott, H., 1914. *Zoological Philosophy*. Translation of Lamarck's *Philosophie Zoologique*. London.
- Elton, C., 1927. *Animal Ecology*. London.
- Engler, A., and Prantl, K., 1889. *Die Natürlichen Pflanzenfamilien*. 4 vols. Leipzig, from 1889 onwards.
- Evolution, 1932. *Evolution in the Light of Modern Knowledge*. A collective work. Cheap ed. London.
- Ewing, H. W., 1916. Eighty-seven Generations in a Parthenogenetic Pure Line of *Aphis avenae*. *Biol. Bull.*, 31, 53.

- Eyster, W. H., 1924. A Genetic Analysis of Variegation. *Genetics*, 9, 372.
- Eyster, W. H., 1928. The Mechanism of Variegation. *Zeits. induct. Abstamm.* —u. VererbLehre. Suppl. 1, 666.
- Eyster, W. H., 1934. The Genetics of *Zea mays*. *Bibliogr. Genet.*, 11.
- Federley, H., 1913. Das Verhalten der Chromosomen bei der Spermatogenese der Schmitterhinge *Pygara anachereta*, *curtula*, und *pigra* sowie einiger ihrer Bastarde. *Zeits. induct. Abstamm.* —u. VererbLehre, 9, 1.
- Federley, H., 1931. Chromosomenanalyse der reziproken Bastarde zwischen *pygara pigra* und *P. curtula* sowie ihrer Rückkreuzungsbastarde. *Z. Zellforsch.*, 12, 772.
- Fernandes, A., 1931. Estudos nos Cromosomas das Liliaceas e Amarilidaceas. *Bol. Soc. Bot. (Coimbra)*, 7, 1.
- Ferrandière, G., 1901. Etudes biologiques sur les zones supralittorales . . . *Bull. Soc. Sci. Nat. Ouest de la France*, 1, 1.
- Finlay, G. F., 1924. The Effect of Different Species Lens Antisera on Pregnant Mice. *Brit. J. Exp. Biol.*, 3, 201.
- Fischer, E., 1902. See Allg. Z. Ent., 6, 363, 377.
- Fischer, E., 1907. Zur Physiologie der Aberrationen und Varietenbildung der Schmetterlinge. *Arch. Rass.* —v. GesBiol., 4, 363.
- Fisher, R. A., 1928. The possible Modifications of the Response of the Wild Type to Recurrent Mutations. *Amer. Nat.*, 62, 115.
- Fisher, R. A., 1930. *The Genetical Theory of Selection*. Oxford.
- Fisher, R. A., 1931. The Evolution of Dominance. *Biol. Rev.*, 6, 345.
- Fisher, R. A., 1934. Professor Wright on the Theory of Dominance. *Amer. Nat.*, 68, 370.
- Fleischmann, A., 1901. *Die Descendtheorie*. Leipzig.
- Fleischmann, A., 1933. The Doctrine of Organic Evolution in the Light of Modern Research. *Trans. Vic. Inst.*, 64.
- Fol, H., 1877. Sur le Commencement de l'énogenie chez divers animaux. *Arch. Sci. nat. et phys. Geneva*, 58.
- Fol, H., 1879. Recherches sur le fécondation et la commencement de l'énogenie. *Mem. Soc. Phys. et d'Hist. nat. Gen.*, 26.
- Ford, E. B., 1923-24. The Geographical Races of *Heodes phleas*. L. *Trans. R. Ent. Soc., London*, 692.
- Ford, E. B., 1930. The Theory of Dominance. *Amer. Nat.*, 64, 560.
- Ford, E. B., 1936. Natural Selection. *Nature*, London, 138, 1053.
- Ford, E. B., 1945. Butterflies. The New Naturalist Series, London.
- Fothergill, P. G., 1936. Somatic Chromosomes in *Urtica*. *Proc. Univ. Durham Phil. Soc.*, 9, 205.
- Fothergill, P. G., 1939. Experimental Genetics in Schools. *Biology*, London, 5, 14.
- Fothergill, P. G., 1941. Evolution: is it proved? *Cath. Her.*, Febr. 28th.
- Fothergill, P. G., 1941b. Evolution: A Question of Fossils. *Cath. Her.*, March 28th.
- Fothergill, P. G., 1941c. Catholics and Evolution. *Cath. Her.*, May 2nd.
- Fothergill, P. G., 1941d. Evolution: Arguments answered. *Cath. Her.*, June 13th.
- Fothergill, P. G., 1941e. Evolution: a Final Letter. *Cath. Her.*, July 7th.
- Fothergill, P. G., 1944. Studies in *Viola* 4. The Somatic Cytology and Taxonomy of our British Species of the Genus *Viola*. *New Phytol.*, 43, 23.
- Fox, R. Hingston, 1919. *Dr. John Fothergill and His Friends*. London.
- Gager, C. S., and Blakeslee, A. F., 1927. Chromosome and Gene Mutations in *Datura* following Exposure to Radium Rays. *Proc. Nat. Acad. Sci. Wash.*, 13, 75.
- Gates, R. R., 1908. See *Nature*, London, 27, 193.
- Gates, R. R., 1933. The General Nature of the Gene Concept. *Nature*, London, 132, 768.

- Gates, R. R., 1936-37. Mutations and Natural Selection. *Proc. Roy. Soc. London, B.*, 121, 56.
- Gaddes, P., 1901. Article on *Biology* in *Chambers' Encyclopedia*, Vol. 2.
- Geitler, L., 1938. Weitere cytogetetische untersuchungen an natuerlichen Populationen von *Paris quadrifolia*. *Zeits. induct. Abstamm.* — u. *VererbLehre*, 75, 161.
- Gerard, 1597. *Natural History of Plants*.
- Gerould, J. H. Blue-green Caterpillars; the Origin and Ecology of a Mutation in Hemolymph Colour in *Colias (Eurymus) philodice*. *J. exp. Zool.*, 34, 385.
- Gershenon, S. M., 1934. Mutant Genes in a Wild Population of *Drosophila pseudoobscura*. *Amer. Nat.*, 68, 569.
- Gesner, C., *Historia Animalium*. 4 vols.
- Goldschmidt, R., 1929. Experimentelle Mutationen und das Problem der sogenannten Paralle-Induktionen. *Biol.Zbl.*, 49.
- Goldschmidt, R., 1931. Analysis of Intersexuality in the Gypsy Moth. *Quat. Rev. Biol.*, 6, 125.
- Goldschmidt, R., 1934. *Lymantria*. *Bibliogr. Genet.*, 1.
- Goldschmidt, R., 1934b. The Influence of the Cytoplasm upon Gene Controlled Heredity. *Amer. Nat.*, 68, 5.
- Goldschmidt, R., 1938. *Physiological Genetics*.
- Goldschmidt, R., 1944. *The Material Basis of Evolution*. 1st ed., 3rd printing, 1944. Yale Univ.
- Goodspeed, T. H., 1929. The Effects of X-rays and Radium on Species of the Genus *Nicotiana*. *J. Hered.*, 20, 243.
- Goodspeed, T. H., and Bradley, Muriel V., 1942. Amphidiploidy. *Bot. Rev.*, 8, 271.
- Goodspeed, T. H., and Olsen, A. A., 1928. The Production of Variation in *Nicotiana* Species by X-ray treatment of Sex Cells. *Proc. Nat. Acad. Sci. Wash.*, 14, 66.
- Gordon, C., 1935. An Analysis of Two Wild *Drosophila* Populations. *Amer. Nat.*, 69, 381.
- Gray, Asa, 1860. Article on Darwinism. *Proc. Amer. Acad. of Arts and Sci.*, 4, 425. 1857-1860.
- Gray, P., and Kirkpatrick, A. F., 1929. Resistant Scale Insects Investigations. *Calif. Citogr.*, part 1, 308, 336; part 2, 364, 380.
- Gray, P., and Kirkpatrick, A. F., 1929b. Resistance of the Black Scale, *Saissetia olea* Bern, to Hydrocyanic Acid Fumigation. *J. Econ. Ent.*, 22, 893.
- Greb, R. J., 1933. Effects of X-radiation on Production of Mosaic Males and on Sex-ratios in *Habrobracon*. *Amer. Nat.*, 67, 88.
- Gregor, J. W. K., 1930. Experiments on the Genetics of Wild Populations. 1. *Plantago maritima* L. *J. Genet.*, 22, 15.
- Gregor, J. W. K., 1931. Experimental Delimitation of Species. *New Phytol.*, 30, 204.
- Gregor, J. W. K., 1938. Experimental Taxonomy 2. Initial Population Differentiation in *Plantago maritima* L. of Britain. *New Phytol.*, 37, 15.
- Gregor, J. W. K., 1939. Experimental Taxonomy 4. Population Differentiation in North American and European Sea Plantains allied to *Plantago maritima* L. *New Phytol.*, 38, 293.
- Gregor, J. W. K., Davey, V. McM., and Lang, J. M. S., 1936. Experimental Taxonomy 1. Experimental Garden Technique in Relation to the Recognition of the Small Taxonomic Units. *New Phytol.*, 35, 323.
- Gross, F., 1932. Untersuchungen über die Polyploidie und die Variabilität bei *Artemia salina*. *Naturwissenschaft.*, 20.
- Grüneberg, H., 1938. An Analysis of the Pleiotropic Effects of a new Lethal Mutation in the Rat (*Mus Norvegicus*). *Proc. Roy. Soc. London, B.*, 125, 123.
- Gulick, A., 1938. What are the Genes? The Genetic and Evolutionary Picture. *Quat. Rev. Biol.*, 13, 1.
- Gulick, J. T., 1872. The Variation of Species as Related to their Geographical Distribution illustrated by the *Achatinellidae*. *Nature*, London. July 18th.

- Gulick, J. T., 1872. Diversity of Evolution Under One Set of External Conditions. *J. Linn. Soc. (Zool.)*, 11, 496.
- Gulick, J. T., 1887. Divergent Evolution Through Cumulative Segregation. *J. Linn. Soc. (Zool.)*, 20, 189.
- Guppy, H. B., 1906. *Observations of a Naturalist in the Pacific*. London.
- Guppy, H. B., 1917. *Plants, Seeds and Currents in the West Indies, Azores*. London.
- Guyenot, E., 1930. *La Variation et L'Evolution*. Paris.
- Guyer, M. F., 1922. Orthogenesis and Serological Phenomena. *Amer. Nat.*, 56, 116.
- Guyer, M. F., and Smith, E., 1918. Studies on Cytolysis 1. Some Prenatal Effects of Lens Antibodies. *J. exp. Zool.*, 26, 65.
- Guyer, M. F., and Smith, E., 1920. Studies on Cytolysis 2. Transmission of Induced Eye Defects. *J. Exp. Zool.*, 31, 171.
- Guyer, M. F., and Smith, E., 1921. Immune Sera and Certain Biological Problems. *Amer. Nat.*, 55, 97.
- Hadley, P., 1927. Microbic Dissociation. The Instability of Bacterial Species with Special Reference to Active Dissociation and Transmissible Autolysis. *J. infect. Dis.*, 40, 1.
- Haeckel, E., 1866. *Generelle Morphologie der Organismen*. Berlin.
- Haemering, J., 1929. Dauermodifikationen. *Handbuch Vererbungsw.*, 1.
- Hagedoorn, A. L., 1911. Autocatalytic Substances the Determinants for the Inheritable Characters. *Vortr. Entw.Mech.Org.*, 12.
- Hakansson, A., 1929. Chromosomenringe in Pisum und ihre Mutmässliche Genetische Bedeutung. *Hereditas*, 12, 1.
- Hakansson, A., 1931. Über Chromosomenverketzung in Pisum. *Hereditas*, 15, 17.
- Hakansson, A., 1935. Chromosomenbedingungen in Einigen Kreuzungen Zwischen Halbsterilen Erbsen. *Hereditas*, 19, 341.
- Haldane, J. B. S., 1930. Theoretical Genetics of Autopolyploids. *J. Genet.*, 32, 339.
- Haldane, J. B. S., 1930b. A Note on Fisher's Theory of the Origin of Dominance. *Amer. Nat.*, 64, 87.
- Haldane, J. B. S., 1932. The Hereditary Transmission of Acquired Characters. *Nature*, London, 129, 817-819 and 856-858.
- Haldane, J. B. S., 1932b. The Inheritance of Acquired Characters. *Nature*, London, 130, 20.
- Haldane, J. B. S. 1932c. The Inheritance of Acquired Characters. *Nature*, London, 130, 204.
- Haldane, J. B. S., 1932d. *The Causes of Evolution*. London.
- Haldane, J. B. S., 1936. Natural Selection. *Nature*, London, 138, 1053.
- Haldane, J. B. S., 1936-37. Primary and Secondary Effects of Natural Selection. *Proc. Roy. Soc. London, B*, 110, 67.
- Hanson, F. B., 1935. Further Data on the Influence of Physiological Differences on the Induced Mutation Rate: Anesthesia, Starvation and Sex. *Amer. Nat.*, 69, 211.
- Hanson, F. B., and Heys, F., 1929. An Analysis of the Effects of the Different Rays of Radium in producing Lethal Mutations in *Drosophila*. *Amer. Nat.*, 63, 201.
- Hanson, F. B., and Heys, F., 1930. A Possible Relation Between Natural (Earth) Radiation and Gene Mutations. *Science*, 71, 43.
- Hanson, F. B., and Heys, F., 1932. Radium and Lethal Mutations in *Drosophila*. *Amer. Nat.*, 66, 335.
- Hanson, F. B., and Heys, F., 1933. Radiation-Genetics (a Review). *Physiol. Rev.*, 13, 466.
- Hanson, F. B., and Heys, F., 1933b. The Effects of Alpha-radiation from Polonium on the Developing Eggs of *Drosophila melanogaster*. *Amer. Nat.*, 67, 567.

- Hanson, F. B., and Heys, F., 1934. The Relation of the Induced Mutation Rate to Different Physiological States in *Drosophila* 3. Irradiation during Rapid as Compared with Slow Germ Cell Formation. *Amer. Nat.*, 68, 97.
- Hardie, R. P., and Gaye, R. K., See Aristotle.
- Harland, S. C., 1936. The Genetical Conception of the Species. *Biol. Rev.*, 11, 83.
- Harris, B. B., 1929. The Effects of Ageing of X-rayed Males upon the Mutation Frequency in *Drosophila*. *J. Hered.*, 20, 299.
- Harris, J. A., 1911. A Neglected Paper on Natural Selection in the English Sparrow. *Amer. Nat.*, 45, 314.
- Harrison, J. W. Heslop, 1920. Genetical Studies in the Moths of the Geometrid Genus *Oporabia* with a Special Consideration of Melanism in the Lepidoptera. *J. Genet.*, 19, 195.
- Harrison, J. W. Heslop, 1926. Miscellaneous Observations on the Induction, Incidence and Inheritance of Melanism in the Lepidoptera. *The Entomologist*, 59, 121.
- Harrison, J. W. Heslop, 1927. Experiments on the Egg-laying Instincts of the Sawfly, *Pontania salicis* Christ. and their Bearing on the Inheritance of Acquired Characters: with some Remarks on a New Principle in Evolution. *Proc. Roy. Soc. London, B.*, 101, 115.
- Harrison, J. W. Heslop, 1928. A further Induction of Melanism in the Lepidopterous Insect *Selenia bilunaria* Esp., and its Inheritance. *Proc. Roy. Soc. London, B.*, 102, 338.
- Harrison, J. W. Heslop, 1928b. Induced Changes in the Pigmentation of the Pupæ of the Butterfly *Pieris napi* L. and their Inheritance. *Proc. Roy. Soc. London, B.*, 102, 347.
- Harrison, J. W. Heslop, 1932. The Inheritance of Acquired Characters. *Nature*, London, 130, 129.
- Harrison, J. W. Heslop, 1935. The Experimental Induction of Melanism, and other Effects, in the Geometrid Moth *Selenia bilunaria* Esp. *Proc. Roy. Soc. London, B.*, 117, 78.
- Harrison, J. W. Heslop, and Garrett, F. C., 1926. The Induction of Melanism in the Lepidoptera and its subsequent Inheritance. *Proc. Roy. Soc. London, B.*, 99, 241.
- Harvey, W., 1651. *De Generatione Animalium*.
- Harvey-Gibson, R. J., 1919. *Outlines of the History of Botany*. London.
- Hedley, Bishop, 1931. Evolution and Faith. In *Evolution and Faith* and other Essays, Ed. by a Monk of Ampleforth, London.
- Heikertinger, F., 1933-36. Kritik der Schmetterlingsmimikry. 1-5. *Biol. Zbl.*, vol 53, 54, 55 and 56.
- L'Héritier, R., and Teissier, G., 1934. Une Expérience de Sélection Naturelle, Courbe d'Élimination du Gène "Bar" dans une Population de *Drosophila* en équilibre. *C.R. Soc. Biol. Paris*, 117, 1040.
- L'Héritier, P., and Teissier, G., 1937. Élimination des Formes Mutantes dans les Population de *Drosophila*. *C. R. Soc. Biol. Paris*, 124, 880.
- Hertwig, O., 1875, 1877 and 1878. Beiträge zur Kenntniss der Bildung Befruchtung und Teilung des Tierischen Eies. *Morph. Jb.*, Leipzig, Vols. 1, 2 and 3.
- Hilaire, Geoffrey, St., 1837. Lectures. Résumé in *Rev. et Mag. de Zool. Paris*.
- Hogben, L., 1930. *The Nature of Living Matter*. London.
- Hollingshead, L., and Babcock, E. B., 1930. Chromosomes and Phylogeny in *Crepis*. *Univ. Calif. Publ. Agric. Soc.*, 6, 1.
- Hortlacher, W. R., and Killough, D. T., 1931. Radiation-induced Variation in Cotton. *J. Hered.*, 22, 253.
- Hough, W. S., 1934. Colorado and Virginian Strains of Codling Moth in Relation to their Ability to enter Sprayed and Unsprayed Apples. *J. Agric. Res.*, 48, 533.



- Hughes, A. W. M., 1932. Induced Melanism in Lepidoptera. *Proc. Roy. Soc. London, B.*, 110, 378.
- Hunter, J., 1861. *Essays and Observations on Natural History, Anatomy, Physiology and Geology*. Posthumous Papers, ed. by J. Owen, London.
- Huskins, C. L., 1931. The Origin of *Spartina Townsendii*. *Genetics*, 12, 531.
- Huskins, C. L., 1941. Polyploidy and Mutations. *Amer. Nat.*, 75, 329.
- Hutton, F. W., 1897. The Place of Isolation in Evolution. *Nat. Sci.*, 11, 240.
- Hutton, F. W., 1899. *Darwinism and Lamarckism*. London.
- Huxley, J., 1936. Natural Selection and Evolutionary Progress. *Rep. Brit. Assoc.*, 1936, p. 81. And in *Nature*, London, 138.
- Huxley, J., 1939. Clines: an Auxiliary Method in Taxonomy. *Bijdr. Dierk.*, 27, 491.
- Huxley, J., 1940. *The New Systematics*. Edited. Oxford.
- Huxley, J., 1942. *Evolution: The Modern Synthesis*. London.
- Huxley, J., and Carr-Saunders, A. M., 1924. Absence of Pre-natal Effects of Lens Antibody in Rabbits. *Brit. J. Exp. Biol.*, 1, 215.
- Huxley, T. H., *Life of Owen*. 2 vols. London.
- Hyatt, A., 1866. In *Mem. Boston Soc. Nat. Hist.*, p. 193.
- Hyatt, A., 1894. Phylogeny of an Acquired Characteristic. *Proc. Amer. Phil. Soc.*, 32, 349.
- Isely, F. B., 1936. Survival Value of Acridian Protective Coloration. *Ecology*, 19, 370.
- Jameson, H. L., 1898. On a Probable Case of Protective Coloration in the House Mouse. *J. Linn. Soc. (Zool.)*, 26, 465.
- Jenkins, F., 1867. Origin of Species. *North Brit. Rev.*, 46.
- Jenkinson, W. J., 1917. *Three Lectures on Experimental Embryology*. Oxford.
- Jennings, H. S., 1906. *Behaviour of the Lower Organisms*. New York.
- Jennings, H. S., 1916. The Numerical Results of Diverse Systems of Breeding. *Genetics*, 1, 53.
- Jennings, H. S., 1916b. Heredity, Variation, etc., in *Diffugia corona*. *Genetics*, 1, 408.
- Jennings, H. S., 1917. The Numerical Results of Diverse Systems of Breeding with respect to two Pairs of Characters linked or independent, with Special Relation to the Effects of Linkage. *Genetics*, 2, 97.
- Jennings, H. S., 1929. Genetics of the Protozoa. *Bibliogr. Genet.*, 5, 105.
- Jennings, H. S., 1930. *The Biological Basis of Human Nature*. New York.
- Jennings, H. S., 1935. *Genetic Variations in Relation to Evolution*. New York.
- Jensen, H. W., 1940. On the Questionable Existence of Sex Chromosomes in the Angiosperms. *Amer. Nat.*, 74, 67.
- Johannsen, W., 1903. *Über Erblichkeit in Populationen und in reinen Linien*. Jena.
- Johannsen, W., 1923. Some Remarks on Units in Heredity. *Hereditas*, 4, 133.
- Johnston, O., and Winchester, A. M., 1934. Studies on Reverse Mutations in *Drosophila melanogaster*. *Amer. Nat.*, 68, 301.
- Jollos, V., 1920. Experimentelle Vererbungsversuchen on Infusorien. *Zeits. indukt. Abstamm. u. Vererb. Lehre*, 35.
- Jollos, V., 1921. Experimentelle Protistenstudien 1. *Arch. f. Protist.*, 45.
- Jollos, V., 1934. Inherited Changes produced by Heat Treatment in *Drosophila melanogaster*. *Genetica*, 16, 476.
- Jollos, V., 1935. Studien zum Evolutionsproblem. *Biol. Zbl.*, 55.
- Jollos, V., 1939. Further Tests of the Role of Cosmic Radiation in the Production of Mutations in *Drosophila melanogaster*. *Genetics*, 24, 113.
- Jones, F. Wood, 1939. *Life and Living*. London.
- Jordan, D. S., 1905. The Origin of Species through Isolation. *Science, N.S.*, 22, 545.

- Jorgensen, G. A., 1928. The Experimental Formation of Heteroploid Plants in the Genus *Solanum*. *J. Genet.*, 19, 131.
- Jorgensen, G. A., 1927. Formation and Morphology of *Solanum* Chimæras. *J. Genet.*, 18, 247.
- Jussieu, A. de, 1789. *Genera Plantarum*.
- Just, E. E., 1932. On the Origin of Mutations. *Amer. Nat.*, 66, 61.
- Kammerer, P., 1913. Das Farbkleid des Feuersalamanders (*Salamandra maculosa* Laurenti) in seiner Abhängigkeit von der Umwelt. *Arch. f. Entwemch. Org.*, 36.
- Kammerer, P., 1923. Breeding Experiments on the Inheritance of Acquired Characters. *Nature*, London, 111, 637.
- Kammerer, P., 1924. *The Inheritance of Acquired Characters*. New York.
- Kane, J., 1896. Observations on the Development of Melanism in *Camplogramma bilineata*. *Irish Nat.*, 5, 74.
- Kant, I., 1914. *Critique of Reason. Critique of Teleological Judgment. Critique of Judgment*. Trans. by J. H. Bernard.
- Karpechenko, G. D., 1927. In *Bull. Appl. Bot. (Plant Breeding)*, 17, 305.
- Kellogg, V. L., 1904. Studies of Variation in Insects. *Proc. Acad. Sci. Wash.*, 6, 203.
- Kellogg, V. L., 1907. *Darwinism Today*. London.
- Kellogg, V. L., and Bell, R. G., 1903. In *Science*, N.S., 28, 741.
- Koken, E., 1902. *Palæontologie und Descendellehre*. Jena.
- Küller, P. Ch., 1936. Cytological Studies on the Reproductive Organs. Chromosome Behaviour in the Male Grey Squirrel (*Sciurus carolinensis leucopus*). *Proc. Roy. Soc.*, 56, 209.
- Kölliker, A. von, 1864. Ueber die Darwin'sche Schöpfungstheorie. *Z. wiss. Zool.*, 14, 174.
- Korschinsky, S. Heterogenesis and Evolution. *Naturw. Wschr.*, 14, 273, 1889; and in Russian in *Bull. Acad. Sci., St. Petersburg*, 10, and in *Flora*, 89, 1901.
- Lamarck, J. B. de, 1809. *Philosophie Zoologique*. Trans. by H. Elliott, 1914, London.
- Lamprecht, H., 1939. Translocation, Gerspaltung und Mutation bei *Pisum*. *Hereditas*, 25, 431.
- Lashley, K., 1916. Results of Continued Selection in *Hydra*. *J. exp. Zool.*, 20, 19.
- Lefevre, J., 1938. *Manuel Critique de Biologie*. Paris.
- Lemoine, P., 1928. Article in *French Encyclopædia*, Vol. 5.
- Leo XIII, Pope, 1879. Encyclical Letter "On the Restoration of Christian Philosophy according to the Mind of St. Thomas Aquinas, The Angelic Doctor." Rome.
- Lesley, J. W., 1928. The Cytological and Genetical Study of Progenies in Triploid Tomatoes. *Genetics*, 13, 1.
- Levit, S. G., 1930. Untersuchungen über Treppenallelomorphismus. 5. *Arch. Entwemch. Org.*, 122.
- Lewitsky, G. A., 1931. The Morphology of the Chromosomes. *Bull. Appl. Bot. (Plant Breeding)*, 27, 19.
- Lillie, F. R., 1927. The Gene and the Ontogenetic Process. *Science*, 66, 361.
- Lindgren, D. L., 1938. The Stupefaction of Red Scale, *Aonidiella aurantii* by Hydrocyanic Acid. *Hilgardia*, 11, 213.
- Lindsay, A. D., 1934. *Kant*. London.
- Lindstrom, E. W., 1933. Hereditary Radium-induced Variations in the Tomato. *J. Hered.*, 4, 128.
- Linnaeus, K., 1735. *Systema Naturæ*.
- Linnaeus, K., 1751. *Philosophia Botanica*.
- Linnaeus, K., 1753. *Species Plantarum*.

- Lacy, W. A., 1908. *Biology and its Makers*. New York.  
 Loeb, J., 1908. Recent Developments of Biology. *Int. Congr. Arts and Scis.*, 9, 13.  
 Lotky, J. P., 1916. *Evolution by Means of Hybridization*. The Hague.  
 Loves, T. E., 1912. *Aristotle's Researches in Natural Science*. London.  
 Lutz, A. M., 1907. In *Science*, 26, 151.  
 Lutz, F. E., 1915. Experiments with *Drosophila ampelophila* concerning Natural Selection. *Bull. U.S. Nat. Mus.*, 34, 605.  
 Lyell, Sir C., 1830. *Principles of Geology*. London.  
 Lyell, Sir C., 1860. *Life and Letters*. Letter to Haeckel, vol., 2, p. 426.  
 MacBride, E. W., 1931. Habit: The Driving Factor in Evolution. *Nature*, London, 127, 933.  
 MacBride, E. W., 1932. The Inheritance of Acquired Characters. *Nature*, London, 129, 900.  
 MacBride, E. W., 1932b. The Inheritance of Acquired Characters. *Nature*, London, 130, 128.  
 MacBride, E. W., 1932c. Chapter on Zoology in *Evolution in the Light of Modern Knowledge*. A Collective Work. Cheap ed., London.  
 MacBride, E. W., 1936. Insect Coloration and Natural Selection. *Nature*, London, 138, 365.  
 MacBride, E. W., 1936b. Natural Selection. *Nature*, London, 138, 884.  
 MacBride, E. W., 1936-37. In Discussion on the Theory of Natural Selection. *Proc. Roy. Soc. London, B.*, 121, 69.  
 MacDougall, M. S., 1929. Modifications in *Chilodon uncinatus*, produced by Ultraviolet Radiation. *J. Exp. Zool.*, 54, 95.  
 MacDougall, M. S., 1931. Another Mutation of *Chilodon uncinatus*, produced by Ultraviolet Radiation with a Description of its Maturation Processes. *J. Exp. Zool.*, 58, 229.  
 Mackenzie, K., and Muller, H. J., 1940. Mutation Effects of Ultraviolet in *Drosophila*. *Proc. Roy. Soc. London, B.*, 129, 491.  
 Malthus, T. R., 1798. *Essays on the Principles of Population*. London.  
 Manwaring, W. H., 1934. Environmental Transformation of Bacteria. *Science*, 79, 466.  
 Marchant, J., 1916. *Alfred Russell Wallace: Letters and Reminiscences*. 2 vols., London.  
 Maritain, J., 1946. *An Introduction to Philosophy*. Trans. E. I. Watkin, Hart Library, London.  
 Marsden-Jones, E. M., and Turrill, W. B., 1938. Researches on *Silene Maritima* and *S. Vulgaris*. *Kew Bull.*, 1928 to 1938.  
 Marsden-Jones, E. M., and Turrill, W. B., 1930-38. Reports on the Transplant Experiments of the British Ecological Society at Potterne, Wilts. *J. Ecol.*, 18, 352, 1930: 21, 263, 1933: 23, 443, 1935: 25, 189, 1937: 26, 359, 1938: 26, 359.  
 Matthew, P., 1831. *Naval Timber and Arboriculture*.  
 Mayr, E., 1942. *Systematics and the Origin of Species*. New York.  
 McAtee, W. L., 1932. The Effectiveness in Nature of the so-called Protective Adaptations in the Animal Kingdom, chiefly as Illustrated by the Food Habits of Nearctic Birds. *Smithsonian Misc. Coll.*, 85, 1.  
 McClintock, B., 1930. A Cytological Demonstration of the Location of an Interchange Between two Non-homologous Chromosomes of *Zea mays*. *Proc. Nat. Acad. Sci. Wash.*, 16, 391.  
 McClintock, B., 1933. The Association of Non-homologous Parts of Chromosomes in the Mid-prophase of Meiosis of *Zea mays*. *Z. Zellforsch.*, 19, 191.  
 McClung, C. E., 1901. Accessory Chromosomes. *Anat. Anz.*, 20, 220.  
 McClung, C. E., 1902. Sex Chromosomes. *Biol. Rev.*, 3, 43.  
 McCullagh, D., 1934. Chromosome and Chromosome Morphology in *Plantaginaceae*. *Genetica*, 16, 1.

- McDougall, W., 1927. An Experiment for the Testing of the Hypothesis of Lamarck. *Brit. J. Psych.*, 17, 267.
- McDougall, W., 1930. Second Report on a Lamarckian Experiment. *Brit. J. Psych.*, 20, 201.
- McDougall, W., 1937. Fourth Report on a Lamarckian Experiment. *Brit. J. Psych.*, 28, 321.
- McKay, J. W., and Goodspeed, T. H., 1930. The Effects of X-radiation on Cotton. *Science*, 71, 633.
- McMurtie, H. See Cuvier.
- Melander, A. L., 1914. Can Insects Become Resistant to Sprays? *J. Econ. Ent.*, 7, 167.
- Mendel, G., 1865. Experiments in Plant Hybridization. *Verh. naturf. Ver. Brünn*, 4. Appeared in 1865. Trans. in Bateson's *Mendel's Principles of Heredity*, 1909, Cambridge.
- Mendel, G., 1869. On Hieracium Hybrids Obtained by Artificial Fertilization. *Verh. naturf. Ver. Brünn*, 8. Trans. in Bateson's Book, see preceding reference.
- Merz, T., 1896-1903. *History of European Thought in the Nineteenth Century*. 3 vols., London.
- Messenger, E. C., 1931. *Evolution and Theology*. London.
- Metchnikov, S., 1924. Sur l'Hérédité de l'Immunité acquise. *C.R. Acad. Sci.*, Paris, 179, 514.
- Michaelis, P., 1937. Untersuchungen zur Problem der Plasmaverbung. *Protoplasma*, 27.
- Mivart, St. George, 1871. *Genesis of Species*. London.
- Mivart, St. George, 1876. *Lessons from Nature*. London.
- Mivart, St. George, 1881. *The Cat*. London.
- Moffett, A. A., 1931. The Chromosome Constitution of the *Pomoideae*. *Proc. Roy. Soc. London, B.*, 168, 423.
- Montgomery, T. H., 1901. A Study of the Chromosomes of Metazoa. *Trans. Amer. Phil. Soc.*, N.S., 20.
- Morgan, C. L., 1896. *Habit and Instinct*. London.
- Morgan, T. H., 1911. Random Segregation versus Coupling in Mendelian Inheritance. *Science*, 34.
- Morgan, T. H., 1912. The Explanation of a New Sex Ratio in *Drosophila*. *Science*, 36, 718.
- Morgan, T. H., 1915. The Role of the Environment. *Amer. Nat.*, 49, 385.
- Morgan, T. H., 1916. *A Critique of the Theory of Evolution*. Princeton Univ. Press.
- Morgan, T. H., 1919. *The Physical Basis of Inheritance*. New York.
- Morgan, T. H., 1926. *The Theory of the Gene*. Yale Univ. Press.
- Morgan, T. H., 1926b. Genetics and the Physiology of Development. *Amer. Nat.*, 60, 487.
- Morgan, T. H., 1927. *Experimental Embryology*.
- Morgan, T. H., 1929. *Mechanism and Laws of Heredity*. *Foundations of Experimental Psychology*. Clark Univ. Press.
- Morgan, T. H., 1932. *The Scientific Basis of Evolution*. New York.
- Morgan, T. H., Bridges, C. B., and Sturtevant, A. H., 1925. The Genetics of *Drosophila*. *Bibliogr. Genet.*, 2 1
- Morley, Wragg, 1939. Ants, Ninth Sense. *Trans. Vic. Inst.*, 71.
- Muller, H. J., 1927. Quantitative Methods in Genetic Research. *Amer. Nat.*, 61, 407.
- Muller, H. J., 1927b. The Artificial Transmutation of the Gene. *Science*, 57, 84.
- Muller, H. J., 1928. Mutation Rate in *Drosophila*. *Genetics*, 13, 279.
- Muller, H. J., 1928c. The Production of Mutations by X-rays. *Proc. Nat. Acad. Sci. Wash.*, 14, 714.

- Muller, H. J., 1929. In *Sci. Monthly*, 19.
- Muller, H. J., 1930. Types of Visible Variations induced by X-rays in *Drosophila*. *J. Genet.*, 22.
- Muller, H. J., 1930b. Radiation and Genetics. *Amer. Nat.*, 69, 220.
- Muller, H. J., 1935. A Viable Two-gene Deficiency. *J. Hered.*, 26, 469.
- Muller, H. J., 1940. *Drosophila* Work on Systematics. In *The New Systematics*. Ed. J. Huxley, pp. 188-191.
- Muller, H. J., and Altenburg, E., 1919. The Rate of Change of Hereditary Factors in *Drosophila*. *Proc. Soc. exp. Biol.*, 17, 10.
- Muller, H. J., and Mott-Smith, L. M., 1930. Evidence that natural radioactivity is inadequate to explain the frequency of "natural" Mutations. *Proc. Nat. Acad. Sci. Wash.*, 16, 277.
- Muller, H. J., and Setlles, F., 1927. The Non-functioning of the Genes in Spermatozoa. *Z. Zellforsch.*, 43, 285.
- Müntzing, A., 1930. Über Chromosomenvermehrung in *Galeopsis*—Kreuzungen und ihre Phylogenetische Bedeutung. *Hereditas*, 14, 153.
- Müntzing, A., 1931. Note on the Cytology of Some Apomictic *Potentilla* Species. *Hereditas*, 15, 166.
- Müntzing, A., 1932. Cytogenetic Investigations on the Synthetic *Galeopsis tetrahit*. *Hereditas*, 16.
- Müntzing, A., 1934. Chromosome Fragmentation in a *Crepis* Hybrid. *Hereditas*, 19, 284.
- Müntzing, A., 1938. Sterility and Chromosome Pairing in Inter-specific *Galeopsis* Hybrids. *Hereditas*, 24, 177.
- Murphy, J. J. *Habit and Intelligence*, Vol. 1.
- Murray, R. H., 1925. *Science and Scientists in the 19th Century*. London.
- Nabours, R., 1930. Mutations and Allelomorphism in the Grouse Locust. *Proc. Acad. Sci. Wash.*, 16, 351.
- Nadson, G. A., 1925. Sur l'accélération du Tempo de la Vie et la Vieillesse prémature chez les Organismes inférieurs sous l'influence des rayons X et du Radium. *C.R. Soc. Biol.*, Paris, 93, 1585.
- Nadson, G. A., and Philipov, G. S., 1925. Influence de Rayons X sur la Sexualité et la Formation des Mutantes chez les Champignons inférieurs (Mucorinées). *C.R. Soc. Biol.*, Paris, 93, 473.
- Nägeli, C. von, 1884. *Mechanisch-Physiologische Abstammungslehre*.
- Navaschin, M., 1925. Morphologische Kernstudien der *Crepis*-Arten im Bezug auf die Artbildung. *Z. Zellforsch.*, 2, 98.
- Navaschin, M., 1926. Variabilität des Zellkerns bei *Crepis*-Arten im Bezug auf die Artbildung. *Z. Zellforsch.*, 4, 171.
- Navaschin, M., 1927. Über die Veränderung von Zahl und Form der Chromosomen infolge der Hybridisation. *Z. Zellforsch.*, 6, 195.
- Navaschin, M., 1931. Spontaneous Chromosome Alterations in *Crepis tectorum* L. *Unif. Calif. Publ. Agr. Sci.*, 6, 20.
- Navaschin, M., 1933. Origin of Spontaneous Mutations. *Nature*, London, 131, 436.
- Newman, H. H., 1935. *Evolution, Genetics and Eugenics*. 2nd ed. Chicago.
- Newman, H. H., and others, 1938. *Twins: A Study of Heredity and Environment*. Chicago.
- Newton, W. C. F., and Pellow, C., 1929. *Primula Kewensis* and its Derivatives. *J. Genet.*, 20, 405.
- Nilsson, H., 1935. The Problem of the Origin of Species. *Hereditas*, 20, 270.
- Nilsson, H., 1939. Der Evolutionsgedanke und die vergangene Pflanzenwelt. *Hereditas*, 24, 377.
- Noethling, W., and Stubbe, H., 1934. In *Zeits. induct. Abstamm.-u. VererbLehre*.
- Nordenskiöld, E., 1929. *The History of Biology*. Trans. by E. B. Eyre. London.

- Ogle, W., 1882. *Aristotle and the Parts of Animals*. London.
- Ogle, W. See Aristotle.
- O'Gorman, P. W., 1941. The Evolution Controversy. *Cath. Her.*, London, April 18th.
- O'Gorman, P. W., 1941b. Evolution: Catholic Writers. *Cath. Her.*, London, May 23rd.
- Oken, L., 1805. *Die Zeugung*.
- Oken, L., 1807. *Program, über die Bedeutung der Schadelknochen*.
- Oken, L., 1809-11. *Lehrbuch der Natur-Philosophie*.
- Olsen, A. R., and Lewis, G. N., 1928. Natural Radioactivity and the Origin of Species. *Nature*, London, 121, 673.
- Osborn, H. F., 1891. Are Acquired Characters Inherited? *Amer. Nat.*, 25, 191.
- Osborn, H. F., 1895. The Hereditary Mechanism and the Search for the Unknown Factors of Evolution. *Biol. Bull. Wood's Hole*, 79.
- Osborn, H. F., 1897. A Mode of Evolution requiring neither Natural Selection nor the Inheritance of Acquired Characters. *Amer. Nat.*, 31, and *Trans. N. York Acad. Sci.*, 1896, 41.
- Osborn, H. F., 1909. *Darwin and Paleontology, Fifty Years of Darwinism*. New York.
- Osborn, H. F., 1924. *From the Greeks to Darwin*. New York.
- Osborn, H. F., 1925. The Origin of Species as revealed by Vertebrate Palæontology. *Science*, 61, 23.
- Osborn, H. F., 1925b. The Origin of Species as revealed by Vertebrate Palæontology. *Nature*, London, 115, 926, and 961.
- Osborn, H. F., 1925c. The Origin of Species, 2. Distinctions between Rectigradations and Aristogenes. *Proc. Nat. Acad. Sci.*, 11, 749.
- Osborn, H. F., 1926b. The Problem of the Origin of Species as it appeared to Darwin in 1859 and as it appears to us today. *Nature*, London, 118, 270, and *Science*, 64, 337.
- Osborn, H. F., 1926c. The Problem of the Origin of Species as it appeared to Darwin in 1859 and as it appears to us today; a Correction. *Nature*, London, 118, 591.
- Osborn, H. F., 1926d. The Origin of Species, 1859-1925. *Bull. Peabody Mus.*, 1, 25, and *Sci. Monthly*, 22, 185.
- Osborn, H. F., 1927. The Origin of Species, 5. Speciation and Mutation. *Amer. Nat.*, 61, 5.
- Osborn, H. F., 1931. The Nine Principles of Evolution revealed by Palæontology. *Rep. Brit. Assoc.*, Sect D., 394.
- Osborn, H. F., 1931b. New Concept of Evolution based upon Researches on the Titanotheres and the Proboscideans. *Science*, 74, 557.
- Osborn, H. F., 1932. The Nine Principles of Evolution revealed by Palæontology. *Amer. Nat.*, 66, 52.
- Osborn, H. F., 1932b. Biological Induction from the Evolution of the Proboscidea. *Science*, 76, 501.
- Osborn, H. F., 1933. Aristogenesis, the observed Order of Biomechanical Evolution. *Proc. Nat. Acad. Wash.*, 19, 699, and 1933b, *Nature*, London.
- Osborn, H. F., 1933c. Biological Inductions from the Evolution of the Proboscidea. *Proc. Nat. Acad. Sci. Wash.*, 19, 159.
- Osborn, H. F., 1934. Aristogenesis, the Creative Principle in the Origin of Species. *Amer. Nat.*, 68, 193.
- Ostergren, G., 1940. Cytology of *Agropyron junceum*, *A. repens* and their spontaneous Hybrid. *Hereditas*, 26, 305.
- O'Toole, G. B., 1933. *The Case against Evolution*.
- Owen, R., 1843. *Lectures on Invertebrate Animals*.
- Owen, R., 1946. Report on the Archetype and Homologies of the Vertebrate Skeleton. Pt. 1. *Rep. Brit. Assoc.*
- Owen, R., 1847. Bones of the Skull in Birds. *Ann. du Mus.*, 10.

- Owen, R., 1855. *Principes d'Ostologie Comparée*. Paris.
- Owen, R., 1858. Presidential Address. *Rep. Brit. Assoc.*
- Owen, R., 1866-68. *Comparative Anatomy and Physiology of Vertebrates*. London, Vols. 1 and 2, 1866. Vol. 3, 1868.
- Packard, A. S., 1894. On the Inheritance of Acquired Characters in Animals with a Complete Metamorphosis. *Proc. Amer. Acad. Arts and Sci. Boston*, 29, 33.
- Packard, A. S., 1901. *Lamarck: The Founder of Evolution. His Life and Work*. London.
- Painter, T. S., 1934. The Morphology of the X-Chromosomes in the Salivary Glands of *D. melanogaster* and a New Type of Chromosome Map for this Element. *Genetics*, 19, 448.
- Painter, T. S., 1935. The Morphology of the 3rd Chromosome in the Salivary Gland of *D. melanogaster*. *Genetics*, 20, 301.
- Painter, T. S., 1939. The Structure of Salivary Gland Chromosomes. *Amer. Nat.*, 73, 315.
- Patterson, J. T., and Muller, H. J., 1930. Are "Progressive" Mutations Produced by X-rays? *Genetics*, 15, 495.
- Payne, F., 1911. *Drosophila ampelophila* Loew. Bred in the Dark for Sixty-nine Generations. *Biol. Bull.*, 21, 297.
- Pearl, R., 1930. The Requirements of a Proof that Natural Selection has Altered a Race. *Scientia*, 47, 175.
- Pearson, H., 1930. *Doctor Darwin, A Biography*. London.
- Pfeffer, G., 1894. *Die Umwandlung der Arten*.
- Phillips, R. P., 1934. *Modern Thomistic Philosophy*. 2 vols. London.
- Philp, J., and Huskins, C. L., 1931. The Cytology of *Matthiola incana*. *J. Genet.*, 24, 359.
- Pictet, A., 1910. Quelques exemplaires de l'Hérédité des Caractères acquis. *Verh. Schweiz. naturf. Ges.*, 93, 272.
- Plate, L., 1903. *Über die Bedeutung des Darwin'schen Selectionprinzips*. Leipzig.
- Plate, L., 1906. Darwinismus kontra Mutations-theorie. *Arch. Rass.—v. GesBiol.*, 3, 183.
- Platt, A. See Aristotle.
- Plough, H. H., and Ives, P. T., 1934. Heat Induced Mutations in *Drosophila*. *Proc. Nat. Acad. Sci. Wash.*, 20, 268.
- Plunkett, C. R., 1927. The Experimental Induction of Melanism in Lepidoptera. *Amer. Nat.*, 61, 821.
- Polimeni, E., 1941. Evolution: The Bergsonian View. *Cath. Her.*, London, May 5th.
- Poole, C. F., 1931. The Interspecific Hybrid *Crepis Rubra* x *C. Foetida* and some of its Derivatives. 1. *Univ. Calif. Publ. Agric. Sci.*, 6, 169.
- Popham, E. J., 1941. The Variation in the Colour of Certain Species of *Arctocoris* (Hemiptera Corixidae) and its Significance. *Proc. Zool. Soc.*, London, 111, 135.
- Poulson, D. F., 1937. Chromosomal Deficiencies and the Embryonic Development of *Drosophila melanogaster*. *Proc. Nat. Acad. Sci. Wash.*, 23, 193.
- Poulson, D. F., 1940. The Effects of Certain X-Chromosome Deficiencies on the Embryonic Development of *Drosophila melanogaster*. *J. Exp. Zool.*, 83, 271.
- Poulton, E., 1897. A Remarkable Anticipation of Modern Views on Evolution. *Sci. Progr.*, N.S.I., 278.
- Poulton, E., 1937. The History of Evolutionary Thought. Presidential Address. *Rep. Brit. Assoc.*
- Poulton, E. B., and Saunders, C., 1899. An Experimental Inquiry into the Struggle for Existence. *Rep. Brit. Assoc.*, 906.
- Przibram, H., 1910. *Experimental Zoologie* 3, *Phylogenese*. Leipzig.

- Punnett, R. G., 1923. Linkage in the Sweet Pea (*Lathyrus odorata*). *J. Genet.*, 13, 101.
- Quatrefages, J. L. A. de, 1892. Charles Darwin et ses Précurseurs français. *Bibliogr. sci.*, 75.
- Quayle, H. J., 1914. Are Scale Insects Becoming Resistant to Fumigation? *Univ. Calif. Publ. Agric. Sci.*, 3, 333.
- Quayle, H. J., 1938. The Development of Resistance to Hydrocyanic Acid in Certain Scale Insects. *Hilgardia*, 11, 183.
- Rabaud, E., 1937. *La Matière vivante et l'Hérédité*. Paris.
- Radt, E., 1930. *The History of Biological Theories*. Trans. by E. J. Hatfield. Oxford.
- Ramsbottom, J., 1941. The Expanding Knowledge of Mycology since Linnaeus. Presidential Address. *Proc. Linn. Soc.*, 151.
- Randolph, L. F., 1932. Some Effects of High Temperature on Polyploidy and other Variations in Maize. *Proc. Nat. Acad. Sci. Wash.*, 18, 222.
- Randolph, L. F., 1941. An Evaluation of Induced Polyploidy as a Method of Breeding Crop Plants. *Amer. Nat.*, 75, 347.
- Ray, John, 1686-1704. *Historia Plantarum*.
- Renouf, L. P. W., 1944. What is Darwinism? *Biol. Health and Sociol.*, ed. Renouf, Cork.
- Rhine, J. B., and McDougall, W., 1933. Third Report on a Lamarckian Experiment. *Brit. J. Psych.*, 24, 213.
- Rhoades, M. M., 1936. The Effect of Varying Gene Dosage on Aleurone Colour in Maize. *J. Genet.*, 33, 347.
- Rhoades, M. M., 1938. Effect of *Dt* Gene on the Mutability of the *a* allele in Maize. *Genetics*, 23, 377.
- Rifenburgh, S. A., 1941. Certain Genetic Effects of Short Wave Ultraviolet Radiations on *Drosophila melanogaster*. *Lloydia*, 4, 65.
- Robbins, R. B., 1918. Applications of Mathematics to Breeding Problems. *Genetics*, 3, 375.
- Roberts, J. A. Fraser, 1940. *Medical Genetics*. London.
- Robson, G. C., and Richards, O. W., 1926. The Species Problem and Evolution. *Nature*, London, 117, 345 and 382.
- Robson, G. C., and Richards, O. W., 1936. *The Variation of Animals in Nature*. London.
- Romanes, G. J., 1897. *Darwin and After Darwin*. 3 vols.
- Rosenberg, O., 1918. Chromosomenzahlen und Chromosomendimensionen in der Gattung *Crepis*. *Arch. f. Bot.*, 15, 1.
- Roux, W., 1881. *Der Kampf der Theile in Organismus*.
- Rückert, F., 1892. Zur Entwicklungsgeschichte des Ovarialeies bei Selachien. *Anat. Anz. Jena.*, 7.
- Rückert, F., 1892b. Ueber die Verdoppelung der Chromosomen im Keimbloschen des Selachiern. *Anat. Anz. Jena.*, 8.
- Russell, B., 1900. *Philosophy of Leibniz: A Critical Exposition*. Cambridge.
- Russell, E. S., 1930. *The Interpretation of Development and Heredity*. Oxford.
- Salisbury, Marquis of, 1894. Presidential Address to the British Association. *Rep. Brit. Assoc.*
- Sansome, E. R., 1932. Segmental Interchange in *Pisum sativum*. *Cytologia*, 3, 200.
- Sansome, E. R., 1932 b. Genetical and Cytological Studies on the Relations between Asiatic and European Varieties of *Pisum sativum*. II. Chromosome Associations in *Pisum*. *J. Genet.*, 25, 35.
- Sansome, F. W., and Philp, J., 1932. *Recent Advances in Plant Genetics*. London.
- Sapelin, A. A., 1930. Röntgen-Mutationen Beim Weizen (*Triticum vulgare*). *Züchter*, 2, 257.



- Schrader, F., 1928. *The Sex Chromosomes*. Berlin.
- Schroder, C., 1903. Über Experimentelle Erzeugte Instinktsvariationen. *Verh. Zool.-bot. Ges. Wien*, 23, 153.
- Schwann, T., 1847. Mikroskopische Untersuchungen über die Uebereinstimmung in der Struktur und dem Wachstum, der Thiere und Pflanzen, Berlin. Trans. in *Sydenham Soc.*, 12, London.
- Scott, D. G., 1908. The Darwin-Wallace Celebration. *J. Linn. Soc.*, London.
- Scott, W., 1894. On Variations and Mutations. *Amer. J. Sci.*, 48, 355.
- Sedgwick, W. T., and Tyler, H. W., 1929. *A Short History of Science*. New York.
- Seeborn, H., 1886. *Physiological Selection*.
- Semon, R., 1912. Das Problem der Vererbung erworbener Eigenschaften. Leipzig.
- Serebrowsky, A. S., 1927. The Influence of the "Purple" Gene on the Crossing-over between "Black" and "Cinnabar" in *D. Melanogaster*. *J. Genet.*, 18, 137.
- Serebrowsky, A. S., 1929. A General Scheme for the Origin of Mutations. *Amer. Nat.*, 63, 374.
- Seward, A. C., 1909. *Darwin and Modern Science*. Edited. Cambridge.
- Sexton, E. W., and Clark, A. R., 1936. Heterozygotes in a Wild Population of *Gammarus chevreuxi* Sexton. *J. Mar. Biol. Assoc.*, 21, 319.
- Shapiro, H., 1932. In *Biol. Bull.*, 63, 457.
- Sharp, L. W., 1934. *Introduction to Cytology*. 3rd Ed., New York.
- Shimotomai, N., 1930. Chromosomenzahlen und Phylogenie bei der Gattung *Potentilla*. *J. Sci. Hiroshima Univ.*, B, 2, 1.
- Short, R., 1935. Some recent Literature concerning the Origin of Man. *Trans. Vic. Inst.*, London, 67.
- Shull, G. H., 1914. Duplicate Genes for Capsule Form in *Bursa Bursa-pastoris*. *Zeits. indukt. Abstamm.* —u. VererbLehre, 12, 97.
- Shull, A. F., 1936. *Evolution*. New York.
- Silfast, J., 1922. Ueber die Beziehungen des Mutterlichen organismus zum Embryo. *Klin. Mbl. Augenheilk.*, 69, 815.
- Singer, C., 1921. *Studies in the History and Method of Science*. 2 Vols. Oxford.
- Singer, C., 1922. *Greek Biology and Greek Medicine*. Oxford.
- Singer, C., 1931. *The Story of Living Things*. New York.
- Singer, C., 1941. *A Short History of Science*. Oxford.
- Sinnott, E. W., and Dunn, L. C., 1925. *Principles of Genetics*. New York.
- Sitko, P., 1938. The Dependence of the Mutational Process on Chromosomal Reconstruction in Translocations. *Mem. Gen. Acad. Sci. Ukrainian S.S.R.*, 2, 31.
- Skousted, A., 1929. Cytological Investigations of the Genus *Aesculus* with some Observations on *Aesculus carnea* Willd, a Tetraploid Species arisen by Hybridization. *Hereditas*, 12, 64.
- Sladden, D. E., 1934. The Transference of Induced Food-habit from Parent to Offspring. Part 1. *Proc. Roy. Soc. London, B.*, 114, 449.
- Sladden, D. E., 1935. The Transference of Induced Food-habit from Parent to Offspring. Part 2. *Proc. Roy. Soc. London, B.*, 119, 31.
- Sladden, D. E., and Hewer, H. R., 1938. The Transference of Induced Food-habit from Parent to Offspring. Part 3. *Proc. Roy. Soc. London, B.*, 126, 30.
- Slaley, R. W., 1942. Chapter on "Science" in the *Legacy of Egypt*, ed. by G. S. R. Granville. Oxford.
- Smith, J. A. See Aristotle.
- Smith, N. K., 1929. *Immanuel Kant's Critique of Pure Reason*. London.
- Smith, W., 1817. *Stratigraphical Systems of Organised Fossils*. London.
- Sonneborn, T. M., 1930. Genetic Studies on *Stenostomum incaudatum* 2. The Effects of Lead Acetate on the Hereditary Constitution. *J. Exp. Zool.*, 57, 409.
- Sonneborn, T. M., 1931. McDougall's Lamarckian Experiment. *Amer. Nat.*, 65, 541.

- Sonneborn, T. M., and Lynch, R. S., 1934. Hybridization and Segregation in *Paramecium aurelia*. *J. Exp. Zool.*, 67, 1.
- Spencer, H., 1910. *First Principles*. Pop. ed., London.
- Spencer, H., 1864. *The Principles of Biology*. London.
- Spencer, H., 1887. *The Factors of Organic Evolution*. Reprint from *Nineteenth Century*, for 1886.
- Spencer, H., 1893-94. Debate between Spencer and Weismann. *Contemp. Rev.*, 1893 and 1894.
- Spencer, W. P., 1932. Vermilion Mutant in *Drosophila melanogaster*. *Amer. Nat.*, 66.
- Spencer, W. P., 1935. The Non-random Nature of Visible Mutations in *Drosophila*. *Amer. Nat.*, 69, 222.
- Stadler, L. J., 1928. Mutations in Barley induced by X-rays and Radium. *Science*, 69, 186.
- Stadler, L. J., 1928b. In *Anat. Rec.*, 41.
- Stadler, L. J., 1928c. Genetic Effects of X-rays in Maize. *Proc. Nat. Acad. Sci. Wash.*, 14, 69.
- Stadler, L. J., 1930. The Frequency of Mutation of Specific Genes in Maize. *Anat. Rec.*, 47, 381.
- Stadler, L. J., 1930b. Some Genetic Effects of X-rays in Plants. *J. Hered.*, 21, 3.
- Stadler, L. J., 1930c. Recovery following Genetic Deficiency in Maize. *Proc. Nat. Acad. Sci. Wash.*, 16, 714.
- Stadler, L. J., 1931. The Experimental Modification of Heredity in Crop Plants 1. *Sci. Agric.*, 11, 557.
- Stadler, L. J., 1932. On the Genetic Nature of Induced Mutations in Plants. *Proc. 6th Int. Congr. Gen.*, 1, 274.
- Stadler, L. J., and Sprague, G. F., 1936. Genetic Effects of Ultra-violet Radium in Maize. 2. Filtered Radiations. *Proc. Nat. Acad. Sci. Wash.*, 22, 279.
- Stancati, M. F., 1932. Production of Dominant Lethal Genetic effects by X-radiation of Sperms of *Habrobracon*. *Science*, 76, 197.
- Standfuss, M., 1898. Experimentelle Zoologische Studien. *N. Denkschr. Schweiz. Ges. Naturw.*, 36, 1.
- Stanford, E., 1872. *The Darwinian Theory and the Law of the Migration of Organisms*. Trans. from Wagner. London.
- Stebbins, G. L., 1938. Cytological Characteristics associated with the different Growth Habits in the Dicotyledons. *Amer. J. Bot.*, 25, 189.
- Stebbins, G. L., 1940. The Significance of Polyploidy in Plant Evolution. *Amer. Nat.*, 74, 54.
- Stein, E., 1922. In *Zeits. induct. Abstamm.*—u. *VererbLehre*, 29.
- Stein, E., 1932. In *Zeits. induct. Abstamm.*—u. *VererbLehre*, 62.
- Stern, C., 1927. Über Chromosomenelimination bei der Taufeliege. *Naturwissenschaften*, 36, 740.
- Stern, C., 1929. Untersuchungen über Aberrationen des Y-Chromosoms von *Drosophila melanogaster*. *Zeits. induct. Abstamm.*—u. *VererbLehre*, 51, 253.
- Stern, C., 1931. Zytologische-genetische untersuchungen als Beweise für die Morgansche Theorie des Faktorenaustauschs. *Biol. Zbl.*, 51, 547.
- Stern, C., 1936. Interspecific Sterility. *Amer. Nat.*, 70, 123.
- Stevens, D. M., 1905. Studies in Spermatogenesis with especial Reference to the Accessory Chromosome. *Corn. Inst. Wash. Pubs.*, No. 36.
- Stewart, G., 1817. *Elements of the Natural History of the Animal Kingdom*. London.
- Stieve, H., 1923. Neuzeitliche Ausichten über die Bedeutung der Chromosomen unter besonderer Berücksichtigung der *Drosophilaversuche*. *Ergeb. Anal. Ent. Gesch.*, 24, 491.
- Stocks, J. L. *Aristotelianism*. London.
- Stocks, J. L. See Aristotle.
- Strasburger, E., 1877. Ueber Befruchtung und Zelltheilung. *Jena. Z. Naturw.*

- Strasburger, E., 1884. *Neue Untersuchungen über den Befruchtungsvorgang bei den Phanerogamen*. Jena.
- Stroer, W. F. H., 1936. The Gene, its Function and its Meaning in Genetics. *Quat. Rev. Biol.*, 11, 57.
- Stubbe, H., 1932. In *Zeits induct. Abstamm.* —u. *VererbLehre*, 60, 474.
- Stubbe, H., 1933. Genmutation. *Handb. Vererbungs- u.*, 2.
- Stubbe, H., 1940. Neue Forschungen zur experimentellen Erzeugung von Mutationen. *Biol. Zbl.*, 60, 113.
- Sturtevant, A. H., 1925. The Effect of Crossing-over at the bar Locus of *Drosophila*. *Genetics*, 10, 117.
- Sturtevant, A. H., 1926. A Cross-over Reducer in *Drosophila melanogaster* due to Inversions of a Section of the third Chromosome. *Biol. Zbl.*, 46, 697.
- Sturtevant, A. H., 1931. Known and probable Inverted Sections of the Autosomes of *Drosophila melanogaster*. *Carn. Inst. Wash. Pubs.*, 42, 1.
- Sturtevant, A. H., 1937. Essays in Evolution 1. On the Effects of Selection on the Mutation Rate. *Quat. Rev. Biol.*, 12, 464.
- Sturtevant, A. H., 1939. High Mutation Frequency Induced by Hybridization. *Proc. Nat. Acad. Sci. Wash.*, 7, 308.
- Sturtevant and Dobzhansky, T., 1936. Inversions in the 3rd Chromosome of Wild Races of *Drosophila pseudo-obscura*. *Proc. Nat. Acad. Sci. Wash.*, 22, 448.
- Sunnner, F. B., 1934. Does "Protective Coloration" protect?—Results of Some Experiments with Fishes and Birds. *Proc. Nat. Acad. Sci. Wash.*, 20, 559.
- Sunnner, F. B., 1935. Evidence for the Protective Value of Changeable Coloration of Fishes. *Amer. Nat.*, 69, 245.
- Sunnner, F. B., 1935b. Studies of Protective Colour Change 3. Experiments with Fishes both as Predators and Prey. *Proc. Nat. Acad. Sci. Wash.*, 21, 345.
- Sunnner, F. B., 1936. Where Does Adaptation Come In? *Amer. Nat.*, 76, 433.
- Sutton, W. S., 1903. The Chromosomes in Heredity. *Biol. Bull.*, 4, 231.
- Sveshnikova, I., 1928. Die Genese des Kerns im Genus *Vicia*. *Zeits. induct. Abstamm. u. VererbLehre. Suppl.*, 2, 1415.
- Tahara, M., 1921. Cytologische Studien an einigen Kompositen. *J. Coll. Sci. Tokyo*, 43, 1.
- Taliaferra, W. H., 1926. Host Resistance and Types of Infections in Trypanosomiasis and Malaria. *Quat. Rev. Biol.*, 1, 246.
- Taliaferra, W. H., 1929. *The Immunology of Parasitic Infections*. New York.
- Tan, C. C., 1935. Salivary Gland Chromosomes in the two Races of *Drosophila pseudo-obscura*. *Genetics*, 20, 392.
- Taylor, A. E., 1925. Section "Philosophy" in *Evolution in the Light of Modern Knowledge*. London.
- Taylor, W. R., 1924. Karyological Studies in *Vicia*. *Bull. Appl. Bot. (Plant Breeding)*, 17.
- Taylor, W. R., 1925. Chromosome Constrictions as Distinguishing Characteristics in Plants. *Amer. J. Bot.*, 12, 238.
- Thompson, D'Arcy Wentworth. See Aristotle.
- Thompson, E., Bell, J., and Pearson, K., 1911. A Third Co-operative Study of *Vespa vulgaris*. *Biometrika*, 8, 1.
- Thompson, W. R., 1937. *Science and Commonsense*. London.
- Thomson, J. A., 1899. The Study of Natural History. Univ. of Aberdeen, Address.
- Thomson, J. A., 1910. *Heredity*, 2nd ed.
- Thomson, J. A., and M. R., 1904. *The Evolution Theory*, 2 vols., trans. of Weismann's *Vorträge über Deszendenztheorie*. London.
- Thomsen, M., and Lemcke, H., 1933. In *Biol. Zbl.*, 53, 541.
- Thorpe, W. H., 1939. Further Studies on Pre-Imaginal Olfactory Conditioning in Insects. *Proc. Roy. Soc. Lond., B.*, 127, 424.
- Timofeeff-Ressovsky, N. W., 1927. Studies on the Phenotypic Manifestation of Hereditary Factors. *Genetics*, 12, 129.

- Timofeef-Ressovsky, N. W., 1931. In *Biol. Zbl.*, 52.
- Timofeef-Ressovsky, N. W., 1931b. Einige Versuche an *Drosophila melanogaster* über die Art der Wirkung des Wirkung des Röntgenstrahlen auf den Mutationsprozess. *Arch. Entomoch. Org.*, 124, 654.
- Timofeef-Ressovsky, N. W., 1931c. Reverse Mutations and Gene Mutations in Different Directions. 2. The Production of Reverse Genovariations in *Drosophila melanogaster* by X-ray Treatment. *J. Hered.*, 22, 67.
- Timofeef-Ressovsky, N. W., 1932. Verschiedenheit der "normalen" Aellele der White-Serie aus zwei Geographisch Getrennten Populationen von *Drosophila melanogaster*. *Biol. Zbl.*, 52, 468.
- Timofeef-Ressovsky, N. W., 1933. Ueber die relative Vitalität von *Drosophila melanogaster* Meigen und *Drosophila funebris* Fab. unter verschiedenen Zuchtbedingungen, in Zusammenhang mit den Verbreitungsarealen dieser Arten. *Arch. Naturgesch.*, 2, 285.
- Timofeef-Ressovsky, N. W., 1934. Ueber den Einfluss des Genotypischen Milieus und der Aussenbedingungen auf die Realisation des Genotype. *Nachr. Ges. Wiss. Göttingen.*, N.F. 1, 163.
- Timofeef-Ressovsky, N. W., 1934b. The Experimental Production of Mutations. *Biol. Rev.*, 9, 411.
- Timofeef-Ressovsky, N. W., 1934c. Ueber die Vitalität einiger Genmutationen und ihrer Kombinationen bei *Drosophila funebris* und ihre Abhängigkeit von "Genotypischen" und vom Aussenen Milieu. *Zeits. indukt. Abstamm.—u. Vererb. Lehre*, 66, 319.
- Timofeef-Ressovsky, N. W., 1935. Über Geographische Temperaturrassen bei *Drosophila funebris*. *Arch. Naturgesch.*, 4, 245.
- Timofeef-Ressovsky, N. W., 1937. *Experimentelle Mutationsforschung in der Vererbungslehre*. Dresden.
- Timofeef-Ressovsky, N. W., 1939. Le Mécanisme des Mutations et la Structure du Gene. *Actual. Sci. Industr.*, 812, Paris.
- Timofeef-Ressovsky, N. W., 1940. Mutations and Geographical Variations in the New Systematics. Ed. J. Huxley, Oxford.
- Timofeef-Ressovsky, H. A., and N. W., 1927. Gentische Analyse einer freilebenden *Drosophila melanogaster*—Populationen. *Arch. Entomoch. Org.*, 109, 70.
- Timofeef-Ressovsky, N. W., Zimmer, K. G., and Delbruch, M., 1935. Über die Natur der Genmutation und der Genstruktur. *S.B. Preuss. Akad. Wiss.*, 6, 189.
- Todd, C., 1930. In *J. Path. Bact.*, 11, 368.
- Torrey, H. B., and Felin, F., 1937. Was Aristotle an Evolutionist? *Quat. Rev. Biol.*, 12, 1.
- Tower, W. L., 1907. Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*. *Carn. Inst. Wash. Pubs.*, 48, 1.
- Treviranus, R., 1802-05. *Biologie oder Philosophie der Lebenden Natur*.
- Tschernak, E., and Bleier, H., 1926. *Ber. Deutsch. Bot. Ges.*, 44, 110.
- Tschetverikov, S. S., 1928. Über die Genetische Beschaffenheit Wilder Population. *Verh. d. v. Int. Kongr. f. Vererb.*, 2, 1499.
- Turesson, G., 1922. The Genotypical Response of the Plant Species to the Habitat. *Hereditas*, 3, 211.
- Turesson, G., 1925. The Plant Species in Relation to Habitat and Climate. *Hereditas*, 7, 147.
- Turesson, G., 1926. Studien über *Festuca ovina* L. *Hereditas*, 8, 161.
- Turesson, G., 1929. Ecotypical Selection in Siberian *Dactylis glomerata*. *Hereditas*, 12, 335.
- Turesson, G., 1930. The Selective Effect of Climate upon the Plant Species. *Hereditas*, 14, 99.
- Turesson, G., 1931. The Geographical Distribution of the Alpine Ecotypes of Some Eurasiatic Plants. *Hereditas*, 15, 329.

- Turrill, W. B., 1933. The Expansion of Taxonomy with Special Reference to *Spermatophyta*. *Biol. Rev.*, 13, 342.
- Turrill, W. B., 1938b. Taxonomy and Genetics. *J. Bot.*, London, 76, 33.
- Turrill, W. B., 1940. Experimental and Synthetic Plant Taxonomy. In *The New Systematics*, ed. by J. Huxley, pp. 47-71, London.
- Upcott, M., 1937. The Genetic Structure of *Tulipa* 2. Structural Hybridity. *J. Genet.*, 34, 339.
- Vialleton, L., 1929. *L'Origine des Etres vivants, L'Illusion Transformiste*. Paris.
- Vilmorin, R. de, and Simonet, M., 1927. Variations du Nombre des Chromosomes chez quelques Solanées. *C.R. Acad. Sci.*, Paris, 184, 164.
- Vilmorin, R. de, and Simonet, M., 1928. Recherches sur le Nombre des Chromosomes chez les Solanées. *Zeits. indukt. Abstamm.—u. VererbLehre. Suppl.*, 2, 1520.
- Virchow, R., 1855. Cellular-Pathologie. *Arch. Path. Anat. Phys.*, 8.
- Vries, H. de, 1901. *Die Mutationstheorie*. Leipzig.
- Vries, H. de, 1905. *Species and Varieties: Their Origin and Mutation*. London.
- Vries, H. de, 1903. Fertilization and Hybridization: In *die Mutations-lehre*, 2, Leipzig.
- Waagen, W., 1869. Die Formenreihe des *Ammonites subradiatus*. *Geog. Jh.*, 2, 139.
- Waddington, C. H., 1939. *Introduction to Modern Genetics*. London.
- Wagner, M., 1868. Über die Darwin'sche Theorie in Bezug auf die Geographische Verbreitung der Organismen. *S.B. bayer. Akad. Wiss.*, p. 359.
- Wagner, M., 1868. *Die Darwin'sche Theorie und das Migrations-gesetz der Organismen*. Leipzig, Trans. by J. L. Baird, 1873.
- Wagner, M., 1870. Über den Einfluss der Geographischen Isolierung und Kolonienbildung auf die morphologischen Veränderungen der Organismen. *S.B. bayer. Akad. Wiss.*, p. 154.
- Wagner, M., 1875. Der Naturprozess der Artbildung. *Auslands-Nachr.*, 22-26 and 29-30.
- Wagner, M., 1880. Über die Entstehung der Arten durch Absonderung. *Kosmos*, 7, 1, 89 and 169.
- Wagner, M., 1889. *Die Entstehung der Arten durch Räumliche Sonderung*. (Collected papers on Isolation).
- Wallace, A. R., 1855. On the Law which has Regulated the Introduction of New Species. *Ann. Mag. Nat. Hist.*, 16, 184.
- Wallace, A. R., 1875. *On Natural Selection*. London.
- Wallace, A. R., 1891. *Natural Selection and Tropical Nature*. London.
- Wallace, A. R., 1892. *Island Life*, 2nd ed. London.
- Wallace, A. R., 1905. *My Life, A Record of Events and Opinions*. 2 vols. London.
- Wallace, A. R., 1909. *Darwinism*. London, 1st ed. 1889; 3rd ed. 1909.
- Walther, H., 1932. In *Int. ent. Z.*, 25, 409.
- Warmke, H. E., 1941. Discussion on Polyploidy. *Amer. Nat.*, 75, 344.
- Watkins, A. E., 1930. The Wheat Species: a Critique. *J. Genet.*, 23, 173.
- Watson, D. M. S., 1936-37. A Discussion on the Present State of the Theory of Natural Selection. *Proc. Roy. Soc. London B.*, 121, 43.
- Watson, E. L. Grant, 1938. Facts at Variance with the Theory of Organic Evolution. *Trans. Vic. Inst.*, 70.
- Watts, W. W., 1932. In *Evolution in the Light of Modern Knowledge*. A collective work. Sect. Geology.
- Webber, J. M., 1930. Interspecific Hybridization in *Nicotiana* XI. The Cytology of a sesquidiploid Hybrid between *Tabacum* and *sylvestris*. *Univ. Calif. Pub. Bot.*, 11, 319.
- Weismann, A., 1887. *Essays on Heredity*.

- Weismann, A., 1892. *Das Keimplasma*. Jena.
- Weismann, A., 1893 and 94. Debate between Weismann and Spencer. *Contemp. Rev.*
- Weismann, A., 1902. *Vorträge über Deszendenztheorie*. Jena. Trans. by J. A. and Mrs. Thomson, London, 1904.
- Weldon, W. E. D., 1899. Presid. Address, Sect. D. *Rep. Brit. Assoc.*
- Wells, H. G., Huxley, J., and Wells, G. P., 1934. *Evolution—Fact and Theory*. Vol. 3, in Science and Life Series. London.
- Wells, W. C., 1813. An account of a White Female part of whose skin resembles that of a Negro. Read in 1813 before the Royal Society, and published in 1818.
- Wenrich, D. H., 1917. Synopsis and Chromosome Organisation in *Chortippus* (*Stenobothrus*) *curtipennis* and *Trimerotropis suffusa* (Orthoptera). *J. Morph.*, 29, 269.
- Wettstein, F. von, 1924. Morphologie und Physiologie des Formwechsels der Mosse auf genetische Grundlage 1. *Zeits. indukt. Abstamm. -u. VererbLehre*, 33, 1.
- Wettstein, F. von, 1926. Über Plasmatische Vererbung sowie Plasma und Genwirkung. *Nachr. Ges. Wiss.*, Göttingen, 68.
- Wettstein, F. von, 1927. Die Erscheinung der Heteroploidie besonders in Pflanzenreich. *Ergeb. Biol.* 2, 311.
- Wettstein, F. von, 1928. Über Plasmatische Vererbung und über das Zusammenwirken von Genen und Plasma. *Ber. Deutsch. Bot. Ges.*, 46, 32.
- Wettstein, F. von, 1932. Bastardpolyploidie als Artbildungsvorgang bei Pflanzen. *Naturwiss.*
- Wettstein, F. von, 1937. Die Genetische und entwicklungs-physiologie Bedeutung des Cytoplasmos. *Zeits. indukt. Abstamm. -u. VererbLehre*, 73, 349.
- Wheeler, W. M., 1923. *Social Life among the Insects*. London.
- White, W., 1847. *History of the Inductive Science*. Vol. 3. London.
- White, M. J. D., 1940. A Translocation in a Wild Population of Grasshopper. *J. Hered.*, 31, 137.
- Whitehead, A. N., 1938. *Science and the Modern World*. Pelican ed. London.
- Whitehead, A. N., 1942. *Adventure of Ideas*. Pelican ed. London.
- Whiting, P. W., 1928. The Production of Mutations by X-rays in *Habrobracon*. *Science*, 68, 59.
- Whiting, P. W., 1929. X-rays and Parasitic Wasps. *J. Hered.*, 20, 269.
- Whiting, P. W., 1932. Mutants in *Habrobracon*. *Genetics*, 17, 1.
- Whiting, A. R., and Bastian, C. H., 1931. The Effects of X-radiation in *Habrobracon*. *Genetics*, 16, 659.
- Whitman, C. D., 1919. Orthogenetic Evolution in Pigeons. *Carn. Inst. Wash. Pubs.*, No. 257.
- Wigand, A., 1874. *Der Darwinismus und die Naturforschung Newtons und Cuviers*. Braunschweig. 3 vols.
- Willis, J. C., 1906. The Flora of Rittigala, a Study in Endemism. *Ann. R. Bot. Grdus. Peradeniya*, 3, 271.
- Willis, J. C., 1916. The Evolution of Species in Ceylon. *Ann. Bot.*, 30, 1.
- Willis, J. C., 1916b. Distribution of Species in New Zealand. *Ann. Bot.*, 30, 437.
- Willis, J. C., 1917. Relative Age of Endemic Species. *Ann. Bot.*, 31, 189.
- Willis, J. C., 1917b. Further Evidence for Age and Area. *Ann. Bot.*, 31, 335.
- Willis, J. C., 1918. Age and Area Hypothesis. *Science*, 47, 625.
- Willis, J. C., 1919. Flora of the Outlying Islands of New Zealand. *Ann. Bot.*, 33, 479.
- Willis, J. C., 1921. Endemic Genera of Plants in their Relation to Others. *Ann. Bot.*, 35, 493.
- Willis, J. C., 1921b. Endemic Genera of Plants. *Ann. Bot.*, 35, 513.
- Willis, J. C., 1922. *Age and Area*. Cambridge.

- Willis, J. C., 1923. Age and Area: a Reply to Criticism. *Ann. Bot.*, 37, 193.
- Willis, J. C., 1940. *The Course of Evolution*. Cambridge.
- Wilson, E. B., 1928. *The Cell in Development and Heredity*. 3rd ed. New York.
- Winchester, A. M., 1934. Studies on Reverse Mutations in *Drosophila melanogaster*. *Amer. Nat.*, 68, 351.
- Windle, B., 1928. *The Church and Science*. London.
- Winge, O., 1917. The Chromosomes, their Numbers and General Importance. *C.R. Lab., Carlsberg*, 13, 131.
- Winuarter, H. de, 1937. Les Chromosomes du genre *Grylotalpa*. *Cytologia Jub. Vol.*, 987.
- Wladimirsky, A. C., 1928. Ueber die Vererbung experimentel erzeugter Förbung von Puppen der Kohlmotte *Plutella maculipennis*. *Biol. Zbl.*, 48, 739.
- Woghum, R. S., 1925. Observations on Insects developing immunity to Insecticides. *J. Econ. Ent.*, 18, 593.
- Wolff, C. F., 1759. *Theorie Generationis*.
- Wolff, G., 1896. Der gegenwärtige Stand des Darwinismus.
- Wolff, G., 1898. *Beiträge zur Kritik der Darwin'schen Lehre*. Leipzig.
- Wollereck, R., 1908. Ueber natürliche und Künstliche Varietätenbildung bei Daphniden. *Verh. Zool-bot. Ges. Wien.*, 18, 234.
- Wollereck, R., 1911. Transmutation und Prainduktion bei Daphnia. *Verh. Zool-bot. Ges. Wien*, 21, 141.
- Wollereck, R., 1928. Ueber die Population Fredericksborgerschloss von *Daphnia cucullata*. *Int. Rev. Hydrobiol.*, 19, 172.
- Wotton, E. *De Differentiis Animalium*.
- Wright, S., 1921. Systems of Mating 1. *Genetics*, 6, 111.
- Wright, S., 1921b. Systems of Mating 2. *Genetics*, 6, 124.
- Wright, S., 1929. Fisher's Theory of Dominance. *Amer. Nat.*, 63, 274.
- Wright, S., 1930. The Genetical Theory of Natural Selection—a Review. *J. Hered.*, 21, 349.
- Wright, S., 1931. Evolution in Mendelian Populations. *Genetics*, 16, 97.
- Wright, S., 1940. Consequences of Mendelian Heredity in Relation to Speciation. In *The New Systematics*, ed. J. Huxley, 161.
- Young, R. J., 1916. Some Experiments on Protective Coloration. *J. exp. Zool.*, 20, 457.
- Tule, G. U., 1924. A Mathematical Theory of Evolution based on the Conclusions of Dr. J. C. Willis. *Phil. Trans. Roy. Soc. London, B.*, 213, 21.
- Zamenhof, S., and Demerec, M., 1943. Studies on the Induction of Mutations by Chemicals. 1. Experiments with Heavy Water (Deuterium Oxide). *Amer. Nat.*, 77, 380.
- Zeleny, C., and Mattoon, E. W., 1915. The Effect of Selection on the "Bar-eye" Mutation in *Drosophila*. *J. Exp. Zool.*, 19, 515.
- Zirkle, C., 1935. The Inheritance of Acquired Characters and the Provisional Hypothesis of Pangenesis. *Amer. Nat.*, 69, 417.
- Zirkle, C., 1936. The Inheritance of Acquired Characters and the Provisional Hypothesis of Pangenesis, Pt. 2. *Amer. Nat.*, 70, 529.

# INDEX

- Abiogenesis, 16, 24;  
Nägeli's, 166-167.
- Abdomen, abnormal in *Drosophila*, 238.
- Acalaphae*, 32, 353, 356.
- Acids, and mutations, 298.
- Acotyledons, 42.
- Action, of predatory birds, 335.
- Ackert, J. E., on pure lines, 190.
- Acquired characters, inheritance of, *see*  
Characters, acquired.
- Acridians, action of selection on, 337.
- Adaptations, 16, 27; allometric, 277, 278;  
Darwinism, a theory of, 346.
- Aegilops ovata*, 218.
- Aegilotriticum*, a new genus, 218.
- Aesculus cornea*, 219.
- Aesculus hippocastanum*, 219.
- Aesculus pavia*, 219.
- Affinity, and analogue, differences, 93;  
genetic, and Kant, 56-57; Lamarck's  
principle of, 70; natural, and Cuvier,  
90.
- Agar, W. E., 268, 368.
- Agassiz, L., 81, 92, 99, 116, 281; and  
Darwinism, 121.
- Age and Area, Willis theory of, 283-285,  
286.
- Aggregata*, cytology of, 246, 247.
- Agol, I. J., 239.
- Agropyron*, 233.
- Albertus Magnus, 35.
- Alcohol and mutations, 298.
- Aldovardi, 37.
- Allelomorphs, 195, 197; multiple, 196,  
242, 290; multiple, in *Drosophila*,  
196; step, 239.
- Allometrons, 277, 278.
- Allopolyploid, 217, 219; in nature, 219.
- Allotetraploid, 219.
- Altenburg, E., on mutations, 303, 305,  
307.
- Amino acids, and gene function, 241.
- Ammonites, as orthogenetic series, 168.
- Amphibians, 43, 71, 357.
- Amphidasys betularia*, 323.
- Amphidiploidy, 216, 218, 219, 220; and  
mutations, 223; production by  
special treatments, 221, 222; true-  
breeding hybrids, 222.
- Analogics, Aristotle's, 23, 32; and Owen,  
92, 93.
- Analogue, definition of, 93.
- Anatomy, aristogenesis and comparative,  
275; classification of animals, 43;  
comparative and Cuvier, 27, 28;  
dissections in human, 60.
- Anaxagoras, 14, 17.
- Anaximander, 13, 14, 17, 46.
- Anaximenes, 13, 14.
- Anchitherium*, 95.
- Ancon sheep, 125, 171.
- Animalculists, 45, 60.
- Anderson, E., 222.
- Aneuploids, 192, 224.
- Antirrhinum*, species, 282, 299; mutation  
in, 304, 307.
- Animals, classification of, 21-24, 43, 50,  
88, 89, 352-360; viviparous and  
oviparous, 354, 357, 358.
- Anura*, 126.
- Aonidiella aurantii*, and selection, 327-328.
- Aphididae*, 45.
- Apogamy, in relation to selection,  
Romanes' definition, 148.
- Aquinas, St. Thomas, 35, 36, 59, 129.
- Arachnids, 359.
- Arcella*, Lamarckian experiments with,  
273, 274.
- Archaeoethism, theory of, 169.
- Archetype, 94; Goethe's, 82.
- Archia caja*, 368.
- Arctocoris distincta*, 329-331.
- Argyll, Duke of, 116; and Darwinism,  
122.
- Aristogenes, 277, 278.
- Aristogenesis, biomechanical evolution,  
Osborn's, 274-280; definition of,  
277.
- Aristotle, 10, 12, 15, 18-33, 34, 35, 36,  
38, 43, 46, 60, 65, 69, 71, 89, 97, 100,  
251, 259, 280, 347; and Cuvier, 89;  
and evolution, 20, 25-33; and ortho-  
genesis, 169; and reproduction, 353;  
and the early classifiers, 38; biology  
of, 21-24; classification of animals,  
31-32, 352-358; concept and theory  
of matter and form, 19, 20, 351-352;  
Thomist view, 20; distinction



- between species and genera, 21;  
*entelechia*, 136; father of scholastic  
 philosophy, 36; founder of system-  
 atic biology, 35; idea of perfection,  
 29, 50; immutability of species, 352;  
 not an evolutionist, 31-32; philo-  
 sophy of, 19, 20, 36; prophet of  
 Darwin, 27; table of classification,  
 355-358.  
 Aristotelians, the Post-, 33-36.  
 Armstrong, H. E., 339.  
 Arsenic, and mutations, 298.  
 Arthropods, co-adaptation in, 156-157.  
*Articulata*, 43, 88.  
 Ascidians, 353, 356.  
 Astauroff, B.L., and mutations, 306.  
 Augustine, St., 35, 279; potentiality of  
 creation, 9, 11.  
 Australia, flora of, 285.  
 Autopolyploid, 217.  
 Autosomes, 207.  
*Avena sativa*, 220.  
 Averroes, 35.  
 Avery, A. G., 229.  
*Aves* (birds), 43, 71, 358, 359.  
 Avicenna, 35.  
 Babcock, E. B., and idiograms in related  
 forms, 193; and mutations, 308.  
 Bacon, F., 38, 52.  
 Bacteria, 273.  
 Baer, K. E. von, 81, 173; and Darwinism,  
 121; discovery of human egg, 100.  
 Baily, J. R., 341.  
 Baldwin, J. M., and organic selection,  
 151.  
 Balcen, of whales, 124.  
 Banta, A. M., on *Daphnia*, 316; on pure  
 lines, 190.  
 Bantams, 337.  
 Barley, mutations in, 238, 306.  
 Barroude, M., and Darwinism, 121.  
 Bartolucci, A., 221.  
 Bary, A. de, 32.  
 Basil, Patristic school of St., 44.  
 Bastian, C. H., and mutations, 306.  
 Bateson, W., 137, 182, 185, 198, 348; and  
 epistasis in mice, 196; and presence-  
 absence hypothesis, 197; evolution-  
 ary theories, 173-174; on sweet pea,  
 194.  
*Batrachus*, 31, 357.  
 Baur, E., 299, 312.  
 Beales, L. S., 102.  
 "Becoming", see "Coming to-be".  
 Beetles, chrysomelid, 368.  
 Beginnings of evolutionary theory, real,  
 59-78, 342.  
 "Being", 44.  
 Beljajeff, M. M., 336.  
 Bell, J., 377.  
 Bell, R. G., 368.  
 Belling, J., on *Datura*, 192, 229.  
 Belt, Thomas, 149.  
 Beneden, P. J. van, 187, 201.  
 Benn, A. W., 25.  
 Bennet, A. W., 123.  
 Berg, L. S., 169, 275, 334; and ortho-  
 genesis, 170; definitions of mutations  
 172.  
 Bergner, A. D., 229.  
 Bergson's, H., *élan vital*, 128, 136.  
 Bernard, Claude, and Darwinism, 121.  
 Bernards, J. H., 54, 55.  
 Bible, the, 49, 50, 97.  
 Bimana, Man, 89, 359.  
*Biologie oder Philosophie der Lebenden Natur*,  
 'Treviranus', 80.  
 Biology, growth of ideas in, 79-81; intro-  
 duction of word, 72.  
 Biophores, Weismann's, ultimate living  
 units, 153-154.  
 Birds, see *Aves*.  
 Bivalents, 229.  
 Bivalves, 253, 356.  
 Black, J., 60.  
 Blackburn, K. B., on *Rosa*, 219; on *Salix*,  
 259.  
 Blainville, Ducratay de, 92, 99.  
 Blakeslee, A. F., 229, 306; on *Datura*, 192  
 Bleier, H., 218.  
 Bonaventure, St., 59.  
 Bonnet, C., and evolution, 45, 46; pre-  
 formation theory of, 45.  
*Botanic Garden*, Erasmus Darwin's, 63.  
 Botany, father of modern, 33.  
 "Boundless" the, 13.  
 Boveri, T., 201, 202, 243; and individu-  
 ality of chromosomes, 188.  
 Boyle, R., 60.  
 Bradley, M. V., 216, 219, 222.  
 Braun, A., and Darwinism, 122.  
 Brecker, L., 370.  
 Bridgeless gap, 292.  
 Bridges, C. B., 298; on *Drosophila sali-*  
*vary glands*, 208.  
 Brink, R. A., 217, 229, 232.  
 Brodie, Sir B., 115.  
 Brogniart, and Darwinism, 121.  
 Brown, R., 101.  
*Bryonia*, 203.

- Bubholz, T. T., and mutations, 306.  
 Büchner, L., and Darwinism, 121.  
 Buckle, H. T., 119.  
 Budge, Dr., 10.  
 Buffering of genes, 238.  
 Buffon, G. L. L., 38, 47-49, 63, 81, 90, 91, 160, 280; and Lamarck, 48.  
 Bumpus, H. C., 377.  
 Burnet, J., 9, 13, 16, 26, 27.  
 Butler, S., 117; and Darwinism, 122, 166; memory theory, 166.  
 Bütschli, O., 102.  
 Buxton, B. H., 218.
- Caesar Cremonini, 19.  
 Camerarius, 40.  
*Camptogramma bilineata*, 377.  
*Campanula persicifolia*, 229, 233.  
 Candolle, A. de and taxonomy, 81.  
*Carausius morosus*, Lamarckian experiment on, 271-272.  
 Carbon bisulphide, 328.  
*Carcinus maenas*, 377.  
 Carothers, E. E., 207.  
 Carpenter, G. D. Hale, and natural selection, 106, 339.  
 Carrick, R., 336.  
 Castle, W. E., on pure lines, 190.  
 Catastrophism, theory of, 87, 98.  
*Catholic Encyclopedia*, 12.  
 Catholic Church, *see* Church.  
 Cavendish, H., 60.  
 Cell theory, the, 100-103, 137, 187; formulation by Schleiden and Schwann, 101-102.  
*Gentaurea nemoralis*, 333.  
 Cephalopods, or *Melachia*, 125, 164, 357.  
 Cesalpino, A., 37, 38-39, 57.  
 Cesnola, A. P. di, on *Mantis*, 335-336.  
*Cetacea*, 31, 125, 354, 358.  
 Ceylon, flora of, 203, 284; hollow curve in, 286.  
*Chaetomium*, mutations in, 304.  
 Chalmers, R. E., and mutations, 306.  
*Chamber's Encyclopaedia*, article on biology in, 108.  
 Chambers, Robert, 79, 98, 123.  
 Chameleons, 126.  
 Change, dynamic, introduction of idea, 14-15; idea of, 347; idea of connected to evolution, 57; of motion, 16.  
 Changes, chromosomal, 215, 216-235; intergenic, 226.
- Characters, inheritance of acquired, and Charles Darwin, 139; and Erasmus Darwin, 68; and Lamarck or Lamarckism, 73-77, 161-163; experiments on, 253-274, 368-370.  
 Chemicals, and induction of mutations, 298-302; used in production of amphidiploids, 221-222.  
 Chen, Dr. Tye Tuan, 9.  
 Chiasma, 209.  
 Chiasmotype theory, Janssens', 209.  
 Chickens, elimination of, 377.  
 Child, G., on *Drosophila*, 238.  
*Chilodon uncinatus*, mutations in, 307;  
 Chinese thought, 9-11.  
 Chloral hydrate, and mutations, 299.  
 Chloroform, and mutations, 299.  
 Christians, the Early, 11, 35.  
 Chromatin, 155; bridges, 233.  
 Chromomeres, 208.  
 Chromosome(s), aberrations and arrangements, 224-235; and reaction systems, 294; appearance in cell division, 192-193; as basis of species change, 288; as bearers of genes, 197-201; as units in heredity, 213; autosomal lethal, 375-377; changes causing variations, 215-216; chemistry, 240-241; evidence for pairing of homologous, 207-211; in species determinations, 190-193; internal arrangements, 225-227; internal arrangements, induction of, 226; maps, in *Drosophila*, 201; maps, in maize, 201; maps, in pea, 201; maps, method of obtaining, 365-368; multivalent associations of, 229; mutations, in *Datura*, 224; pairing in hybrids, 217-218; pattern in evolution, 235, 292; sex, and CIB technique, 371-374; sex, attached X's, 374; sex, in *Aggregata*, 246-247; sex, Jensen's criticisms of, 244; sex, mechanism of, 202-206, 207; theory, criticisms of, 241-250; theory, cytological evidence for, 201-211; theory, of heredity, 197-201; theory, of indirect binding, 217-218; ultimate unit of, 235-238; *Y* role in inheritance, 206.  
 Chromosomin, 240.  
*Chrysanthemum*, chromosome numbers in, 191.  
 Church, Catholic, 20, 36; 120; Early Fathers of, 11, 34.  
 Ciona, 368.

- Circotettix*, unequal chromosomes in, 207.  
*Cirripedes*, 359.  
 Clark, A. R., on wild populations of *Gammarus*, 311.  
 Classification, 39-44, 50; according to Aristotle, 21-24, 352-358; according to Cuvier, 38-39, 57; according to Cuvier, 43, 88-89; according to Hunter, 50-51; according to de Jussieu, 42; according to Lamarck, 70, 358-360; according to Linnaeus, 40, 41, 43, 57, 71.  
 CIB technique for measuring mutation rate, 371-377.  
 Clausen, J., 64, 221.  
 Cleland, R. E., 229.  
 Cline, 290.  
 Clodd, E., 64.  
 Co-adaptation, in bees, ants, arthropods, 156.  
 Cobra, hood of, 124.  
*Coccus pseudomagnoliarum*, 328.  
 Coelenterates, 353.  
 Cole, F. J., 60.  
*Colias philodice*, 336-337.  
 Collingwood, R. G., 128.  
 Collins, J. L., and mutations, 308; on recessive gene in barley, 238.  
 Coloration, warning, 333-339.  
 "Coming-to-be" ("becoming"), 44, 347, 351.  
 Confucius, 9, 10.  
 Consciousness, as a factor in orthogenesis, 170.  
*Contemporary Review*, 140.  
 Contraries, the, 351.  
 Cooper, D. C., 229, 232.  
 Cope, E. D., 164, 252; and Darwinism, 121, 140, 169, 173; and Lamarckism, 162, 164.  
 Copper sulphate, and mutations, 298.  
 Copernicus, 60.  
 Cordus, Valerian, 34.  
*Corixa*, 329.  
 Correns, C., 8, 102, 138, 182, 202.  
 Cott, H. B., 333, 334, 338, 339.  
 Cotton, mutations in, 306.  
 Coulter, J. M., 8.  
 Crampton, H. E., on *Philosamia*, 324-325.  
 Crane, M. B., 191.  
 Creation, 11, 128, 129-130; derivative, 344; Mosaic account of, 34, 50, 79; special, 48, 109, 347; special and Cuvier, 87, 91; special and Darwin, 129; special and Dewar, 347; special and Owen, 95.  
 Creator, The, 5, 11, 41, 52, 55, 57, 65, 66, 80, 82, 96; and fossils, 97.  
 Creighton, H. B., cytology of *Zea*, 209-211.  
*Crepis alpina* x *tectorum* hybrids, 207; *divaricata* x *diocorides* hybrids, 223; polysomes in, 224; polyploidy in, 222-223; *rubra* x *foetida* hybrids, 220.  
 Crew, F. A. E., definition of gene, 236; and McDougall's work on Lamarckism, 268-270.  
*Critique of Judgment*, Kant's, 55, 56, 61.  
*Critique of Reason*, Kant's, 54.  
*Critique of Teleological Judgment*, Kant's, 54.  
 Cross breeding, swamping effects of, 132, 146.  
 Crossing-over, determination of amount of, 364-368; effect of inversions on, 234; linkage in *Drosophila*, 198-200; suppressor, 371, 372.  
 Crustacea, or *Malacostruca*, 356.  
 Cryptogams, 41.  
 Culture, Arab, 35; Babylonian, Chinese and Egyptian, 9-11.  
 Cunningham, J. T., 169, 253, 256, 257.  
 Curve, Willis' hollow, 286.  
 Cuvier, G. L., 43, 61, 77, 81, 86-90, 91, 92, 95, 97, 99; analytic method of study, 88; and contemporaries, 90-92; and fossils, 97; and foundation of palaeontology, 87; and Special Creation, 87, 91; classification of animals, 88-89; definition of species, 88.  
 Cycadophytes, mesozoic, 282.  
 Cytogenetics, and evolution, 212-250; and translocations, 228-233; linkage of cytology and genetics, 103, 187.  
 Cytology, 100; linked with genetics, 103.  
 Cytoplasm, importance in development, 243.  
 Cytoplasmic inheritance in *Ephelobium*, 245; in *Lymantria*, 243; in mosses, 243.  
*Dactyloctenium pictum*, 337.  
 Dallinger, on *Infusoria*, 273.  
 Dalton, J., 6.  
 Dampier, Whetham, 62.  
 Danilevsky, N. J., 173.  
*Daphnia*, 316, 368.  
 Dark Age, the, 34.  
 Darlington, C. D., 47, 103, 201, 203, 207, 209, 216, 218, 226, 229, 233, 235; definition of meiosis, 188.

- Darwin, Charles, 4, 5, 6, 43, 44, 61, 62, 63, 68, 75, 80, 98, 104-134, 137, 138, 139, 140, 141, 142, 155, 171, 172, 173, 174, 176, 280, 319, 341, 343, 346, 348; and Lamarck(ism), 105; and Origin of Species, 25, 52, 61, 99, 106-111, 113, 114, 115, 116, 119, 121, 123, 129, 131, 132, 135, 144; anticipation of, by Prichard, 83-86; beginnings of his evolutionary thought, 106-107; greatest contribution to science, 105; laws of Beauty and Battle, 144; theory of pangenesis, 152, 241.
- Darwin, Erasmus, 61, 62-68, 160, 280; and evolution, 63, 64; and spontaneous generation, 64; and the "living filament", 66-67; inheritance of acquired characters, 66-67; *Temple of Nature*, 63, 64; *The Botanic Garden*, 63; *Zoonomia*, 63, 65, 66, 67.
- Darwin, Francis, 107; and Prichard's views, 83, 85.
- Darwinism, 104-134, 166, 168, 181, 288, 290; a theory of adaptations, 346; and mutation theory, 171, 310, 318; and orthogenesis, 275; as a theory, 105, 111-115, 346; difficulties confronting, 124; founded on observation, 110; general and special criticisms of, 122-128, 132-134; Jenkins' criticism of, 132-133; Korschinsky's criticism of, 133-134; literature of, 115, 119; reception of, 115-122; rejected by Owen, 96; strength of appeal of, 109-111; see also Neo-Darwinism.
- Datura stramonium*, cytology of, 192; mutations in, 306; translocation in, 230; trisomics in, 224, 229.
- Daudin, H., 87.
- Dauermodification*, Jollos', 274.
- Davenport, C., 377.
- Davey, V. McM., 332.
- Davies, J. R. Ainsworth, 31, 115, 121.
- Davies, L. Merson, 347.
- De Anima*, Aristotle's, 18, 19, 20, 29, 30, 33, 352, 354.
- De Caelo*, Aristotle's, 13, 18, 351.
- De Causis Plantarum*, Theophrastus', 33.
- De Differentiis Animalium*, Wotton's, 37.
- De Generatione Animalium*, Aristotle's, 18, 24, 30, 32, 353, 354.
- De Generatione Animalium*, Harvey's, 100, 353, 354, 355, 356, 357, 358.
- De Generatione et Corruptione*, Aristotle's, 18, 20, 351, 352.
- De Partibus Animalium*, Aristotle's, 18, 21, 22, 24, 26, 28, 353-356.
- De Plantis Libri*, Cesalpino's, 38.
- Deficiency, chromosome, 225, 226, 227.
- Delage, Y., 159; and Darwinism, 121.
- Delaunay, L. N., idiograms in related forms, 193.
- Delbrück, M., and mutations, 310.
- Deletion, chromosome, 227.
- Dembowski, J., 245.
- Demerec, M., 298, 314; and mutations, 309; and genes, 312.
- Democritus, 6, 14, 15, 17, 34, 47, 352.
- Dermen, H., 222.
- Descartes, R., 38, 52, 54, 57, 118, 128.
- Desoxyribose nucleic acid, 240.
- Determinants, Weismann's, 153-155.
- Detlefsen, J. A., 253.
- Deuterium oxide, induction of mutations, 298-299.
- Dewar, D., 342, 347.
- Dichotomy, Lamarck's, of animals, 72.
- Dickson, C., 328.
- Dicotyledons, 42.
- Diderot, D., 38, 44, 47, 61.
- Differentiation, evolution by, 285-288.
- Digby, L., 219.
- Digitalis ambigua*, 218.
- Digitalis Martonensis*, a new "species", 218.
- Digitalis purpurea*, 218.
- Diogenes of Appollonia, 14.
- Dioscorides, 34.
- Diploid organism, 191.
- Diptera*, inversions in, 233-234; salivary gland chromosomes, 293.
- Direction and course of science, 51.
- Diver, C., on natural selection, 106, 340.
- Dobell, C., criticisms of gene theory, 246-248.
- Dobroval'skaia-Zavad'skaia, N.A., on mutations, 306.
- Dobzhansky, T., 226, 232, 234, 293, 295, 299, 313, 318, 329, 332, 341; and selection, 320.
- Doctor, The Angelic, 36.
- Dogma, of Creation, 129-130.
- Dominance, Fisher's theory of, 317; genetic, 184; imperfect, in *Mirabilis*, 194.
- Doncaster, L., on criss-cross inheritance, 203.
- Driesch, Hans, 54, 196, 202; and Darwinism, 121, 246, 247, 248, 296, 298, 299.

- 304, 305, 306, 307, 316, 331, 332, 341.
- Drosophila*, 246, 247, 248, 296, 298, 299, 304, 305, 306, 307, 316, 331, 332, 341; and natural radiations, 308-309; and temperature, 302-303; chromosome deficiencies, 227; chromosome duplications in, 228; chromosome translocations in, 229; criss-cross inheritance in, 204; crossing-over and chromosome maps, 364-368; gene combinations in, 236; genetics of, 296-297; lethals in, 315; measurement of mutation rate, 371-377; multiple allelomorphs of, 196; mutations in wild populations, 311; mutation of eye-colour in, 309; mutations of eggs and sperms, 309; reverse mutations in, 313; salivary gland chromosomes, 208; statistical analysis (of sex ratio) in, 363-364; virgin females, 297.
- Drosophila azteca*, 234, 293.
- Drosophila funebris*, 314, 316, 332; "radius incompletus", 237; viability of mutants in, 316.
- Drosophila hydei*, 314.
- Drosophila melanogaster* (*ampelophila*), 197, 208, 209, 227, 228, 233, 236, 254, 297, 298, 299, 304, 311, 313, 315, 322; linkage in, 198-201.
- Drosophila miranda*, chromosomes in, 234.
- Drosophila pseudobscura*, 293, 298, 332, 341; chromosomes in, 234.
- Drosophila simulans*, 298.
- Dualism, of Descartes, 128; of Scotus, 59.
- Dubinim, N. P., 239, 293, 311.
- Dudycha, G. J., 10, 11.
- Duerden, J. E., and callosities of ostrich, 254.
- Duggar, B. M., 296.
- Dujardin, Felix, 47, 101.
- Dumas, 152.
- Duncan, F. B., 298.
- Dunn, L., 215.
- Duplication, chromosome, 225, 227-228.
- Duret, 44.
- Durham, F. M., on epistasis in mice, 196.
- Dürkhen, B., on *Pieris*, 369-370.
- Dynamists, 14.
- East, E. M., 64; and mutations, 317.
- Esthelle*, 46.
- Ecotypes, 332.
- Edison, Thomas, 62.
- Edwards, H. Milne, 86; and Darwinism, 121.
- Effect, directional in mutations, 309; position, 294.
- Egg, Aristotle's definition of, 354-355.
- Egyptians, Ancient, 9, 10.
- Eimer, Th., 140, 168, 169; and Darwinism, 121; and Lamarckism, 162.
- Einstein, A., 55.
- Elan vital*, Bergson's, 128, 136.
- Elements, primary, 9, 10, 13, 14, 15, 16, 351.
- Elephant, 274, 277, 278; fossil, orthogenetic series, 168.
- Ellenhorn, J., 208.
- Elliott, Hugh, 69, 70, 72, 73, 74, 75, 76.
- Elton, C., 339.
- Embryology, 79; and aristogenesis, 275; founded by van Baer, 101.
- Empedocles, 10, 14, 15-17, 25, 26, 27, 280, 351.
- Encasement, doctrine of, 45.
- English oysters, mutation in, 125.
- Entelechy, 53, 128, 280.
- Epicurus, 34.
- Epigenesis, 100.
- Epilobium luteum* x *E. hirsutum* hybrid, 243.
- Epistasis, in mice, 196.
- Equisetals*, 282.
- Equus*, 95, and see Horse; fossil series, 168.
- "Erasmism", 68.
- Ether, and mutations, 298.
- Ethylene oxide, 328.
- Euphydryas aurinta*, 323.
- Eve, formation from Adam, 67.
- Evolution, a dynamic process, 288; a fact, 347, 349; a philosophy, 342; a working hypothesis, 345; and Aristotle, 25-33; and Erasmus Darwin, 62-68; and mutations, 289-295, 315-319; and origin of life, 343-344; and scientific methodology, 344; biomechanical, or aristogenesis, 274-280; Bonnet's idea of, 45; classical evidence for, 343; conception of, 3, 4, 5; connected to idea of change, 57; cosmic (cosmological), 11, 343, 344; created, 280; creative, 280; cumulative effect of evidence for, 117, 343, 345; direct evidence for, 349; Empedocles' views of, 15-17; establishment as a principle, 135-140; idea of, 51; importance of chromosome theory to, 197; nothing repugnant in idea of, 345; summary of history of, 347-349.

- Evolutionism, 349.  
 Ewing, H. W., on pure lines, 190.  
 Existence, struggle for and Darwin, 112-114.  
 Extrachromatin, in *Pyrrhocoris*, 202.  
 Eye, origin of, and Darwinism, 124.  
 Eye colour, in *Drosophila*, 196.  
 Eyster, W. H., 239; on chlorophyll in maize, 196.  
  
 Factors, 206; *see also* "Gene"; duplicate and dominant, 195.  
 Fallopius, 97.  
 Federley, H., on *Pygaera*, 207.  
 Felin, F., 25, 26, 30, 33.  
 Fernandes, A., and frequency graphs, 216-217.  
 Ferronière, G., 368.  
 Filaments, Erasmus Darwin's living, 66, 67.  
 Finlay, G. F., 369.  
 First Cause, 33.  
 Fischer, E., 368.  
 Fisher, R. A., 290, 316, 317, 322; on pure lines, 190.  
 Fishes, 28, 31, 71, 99, 359.  
 Fleischmann, A., opponent of evolution, 135, 347.  
*Flora of Ceylon*, Trimen's, 283.  
 Flourrens, P., and Darwinism, 121.  
 Flower, in classification, 39, 40; parts, as modification of leaves, 82.  
 Fol, H., 187, 201.  
 F<sub>1</sub> and F<sub>2</sub> hybrid generations, 360-363.  
 Force, Empedocles' attraction and repulsion, 16.  
 Ford, E.B., 317, 323, 339.  
 Form, *see* Aristotle, accidental and substantial; whole-natured, 26.  
 Formulative period of evolution, 59-178, 342.  
 Fossils, and evolutionary theories, 274-275.  
 Fothergill, Dr. John, 40.  
 Fothergill, P. G., 347; and idiograms in related forms, 193.  
 Fox, white arctic, and Darwinism, 339.  
 Fox, R. Hingston, 40.  
  
 Gamma-rays, in production of mutations, 306, 309.  
 Gager, C. S., on mutations, 306.  
 Gairdner, A. E., 229, 233.  
  
 Galen, 34, 60.  
*Galeopsis pubescens*, 219.  
*Galeopsis speciosa*, 219.  
*Galeopsis tetrahit*, synthetic, 219.  
 Galileo, 19, 60.  
 Galleria, 370.  
*Gambusia*, 334-335.  
 Gametes, 360.  
 Gametic coupling and repulsion in sweet pea, 194, 198.  
*Gammarus chevreuxi*, 311.  
 Garden, Royal Botanic, at Kew, 40.  
 Gartner, J., 182.  
 Garrett, F. C., 299, 300.  
 Gates, R. Ruggles, and natural selection, 106, 216, 245.  
 Gaye, R. K., 26.  
 Geddes, Patrick, 108.  
 Gegenbauer, C., and Darwinism, 121.  
*Genera Plantarum*, A. de Jussieu's, 42.  
*General History of Plants*, Gerard's, 37.  
 Gene, 206, 207, 212, 213, 214, *see also* Factors, Mendelian factors; a morphological concept, 242; and cytoplasmic action, 243-244; as autocatalysts, 239, 240; at a chromosome locus, 201; bar, 228; chemical nature and functions of, 238-241; complex, 237-238; criticisms of theory of, 241-250; definition of, 236; derivation of theory of, 241; functions and amino acids, 240-241; general features of, 235-238, 360-362; germinal selection of lethal, 309; Goldschmidt and idea of, 294-295; interaction of, 237; lethal, 27, 227, 375-377; lethal, in *Drosophila*, 315, 316, 317; lethal, accumulation and mutation rate, 375-377; mutations and evolution, 289-295; mutation(s) deleterious, 289; pleiotropic, in *Drosophila*, 313.  
 Generation, spontaneous, 16, 24, 167.  
 Genesis, literal interpretation of, 109.  
 Genetic systems, theory of, 242.  
 Genetics, 348; developed from Mendelism, 186; of *Drosophila*, 296, and *see Drosophila*.  
 Genomeric theory, Eyster's, 239.  
 Genotype, 361.  
 Geoffrey, M., 75.  
 Geology, and evolution, 97-100, 282.  
 Gerard, 37.  
 Germ plasm, definition, 360; Weismann's theory of, 152-160.  
 Gerould, J. H. 336.

- Gershenson, S. M., on wild populations of *Drosophila*, 311.
- Gesner, 37, 43, 57.
- Gibson, K. J. Hurvey, 33.
- Glacial, age, 291.
- Glyptodon, 126.
- Godron, Dr., 173.
- Goethe, J. W. von, 8, 81, 90, 92, 104; introduction of word morphology, 81; theory of evolution, 81-82; unity of type theory, 82.
- Goette, A., and Darwinism, 121.
- Goldschmidt, M., 159.
- Goldschmidt, R., 198, 241, 281, 303, 310, 348; and cytoplasmic inheritance, 243; characteristics of genes, 239-240; ideas of micro- and macro-evolution, 288-295.
- Goodspeed, T. H., and mutations, 216, 218, 219, 222, 306.
- Gordon, C., on wild populations of *Drosophila*, 311.
- Gracilaria stigmatella*, 368-369.
- Graminæ, 39.
- Grasshoppers, 229, 233.
- Gray, Asa, 114.
- Gray, P., 328.
- Greb, R. J., and mutations, 306.
- Greek and Mediaeval period of evolution, 7, 11-36, 342.
- Gregor, J. W. K., 332.
- Grouse locust, 314.
- Grub, Aristotle's comparison with egg, 354-355.
- Gryllotalpa grylloides*, geographic races of, 293.
- Gryphaea*, 274, 303.
- Gulick, J. T., 165; and geographical isolation, 147-148.
- Guppy, H. B., evolution by differentiation, 287.
- Guyenot, E., 347.
- Guyer, M. F., on serology, 369.
- Haacke, W., on Darwinism, 121.
- Haberlandt, G., 121.
- Hadley, P., 273.
- Haeckel, E. von, 80, 98, 121, 128, 136, 360.
- Haernerling, J., 243.
- Hagedoorn, A. L., 240.
- Hakansson, A., 229.
- Haldane, J. B. S., 103, 215, 223, 290; and MacBride, 255; and theory of dominance, 317; disagreement with Harrison & MacBride, 260; on natural selection, 106, 339.
- Hanson, F. B., on *Drosophila*, 297, 306, 308, 309, 310.
- Haploid organism, 192.
- Haploids, pairing of chromosomes in, 208.
- Hartel, R. P., 26.
- Harland, S. C., on cotton, 298.
- Harris, B. B., and mutation, 3.
- Harrison, J. W. H., 263, 289; and induced mutations, 299-302; and MacBride, 255; on *Oporabia autumnata*, 325-327; on *Pieris napi*, 369-370; on *Rosa*, 219; on Sawfly (*Pontania*), 258-261.
- Hartmann, E. von. and Darwinism, 121.
- Hartsoecker, 45.
- Harvey, W., 60, 100.
- Hawaiian flora, 285.
- Heodes phlaeas*, 323.
- Hedley, Bishop, and the Patristic School of St. Basil, 44.
- Heikertinger, F., 339.
- Henking, H. von, 188, 201, 202.
- Henslow, G., and Darwinism, 121, 122.
- Heraclitus, 12, 14, 15.
- Hermes, Vision of, 11.
- Heron, night, 335.
- Hertwig, O., 102, 201; and fertilization, 187.
- Heterogenesis, and evolution, 133-134; or mutation theory of evolution, 170-178.
- Heterosis, 361.
- Heterozygote, translocation, 229.
- Hewer, H. R., on *Carausius*, 271-272.
- Hexaploid, 219.
- Heys, F., on *Drosophila*, 297, 306, 308, 309, 310.
- Hiesey, W. M., 332.
- Hipparion*, 95.
- Hippocrates, 17, 251.
- Histoire Naturelle*, Buffon's, 48.
- Historia Animalium*, 18, 21, 22, 23, 28, 30, 34, 353, 354, 355, 356, 357, 358.
- Historia Animalium*, Gesner's, 37.
- Historia Plantarum*, Ray's, 39.
- Historia Plantarum*, Theophrastus, 33.
- Historia Stirpium*, Valerian Cordus', 34.
- Hogben, L., and principles of evolution, 342.
- Hollingshead, L., and idiograms in related forms, 193.
- Holothurians, 32, 353, 356.
- Homogamy, definition by Romanes', 148.

- Homology, 50, 95, 96, 97, 127; and G. St. Hilaire, 92; and Owen, 92-94.  
 Homologue, definition of, 93.  
 Homozygote, translocation, 229-232.  
 Homunculus, the, 45, 100.  
 Hooke, Robt., introduction of word cell, 100.  
 Hooker, Sir W. J., 83, 107, 114, 115, 122.  
 Horlacher, W. R., and mutations, 306.  
 Horse, 274, 277, 354, *see also Equus*.  
 Hughes, A. W. M., 301-302.  
 Hunter, John, 49, 51, 87; system of classification, 50.  
 Huskins, C. L., 221, 229; and chromosome aberrations, 223-224.  
 Hutton, F. W., 132, 253, place of isolation in evolution, 150.  
 Huxley, J. S., 61, 119, 151, 226, 232, 235, 295, 311, 315, 319, 333, 342, 349, 369; and Harrison's work on *Pontania*, 261; and natural selection, 109; on character differences, 238; on experiments on *Carausius*, 271.  
 Huxley, T. H., 91, 99, 118, 119, 120, 121, 173; as Darwin's advocate, 115; on protoplasm, 101.  
 Hyatt, A., as a Neo-Lamarckian, 164, 276.  
 Hybrids, backcross, 361-362; F<sub>1</sub> and F<sub>2</sub>, 360-362; intergeneric, 218, 222; interspecific, 218-223.  
 Hydrogen cyanide, 329.  
*Ichthyosauria*, 125.  
 Idants and ids, Weismann's, 153-157.  
 Idiograms, in systematics, 192-193.  
 Idioplasm, or germ plasm, Weismann's, 153-160; Nägeli's, 167.  
 Incipient stages, and natural selection, 124.  
 India, flora of, 283, 284.  
*Infusoria*, 46, 70, 101, 358; Lamarckian experiments with, 273.  
 Inheritance, criss-cross, 203-204.  
*Insecta* (insects), 24, 31, 43, 71, 356, 359.  
 Intelligence, The Divine, 11, 127.  
 Inversion, chromosome, 226, 233-235; and crossing over, 234.  
*Invertebrata*, 71, 72.  
 Ionian School of Philosophy, Early, 12-14; Later, 14-18.  
 Ireland, Mr., 79.  
 Isely, F. B., on acridians, 337.  
 Isolation theories, 145-150.  
 Ives, P. T., and mutation rates, 303-304.  
 Jamaica, flora of, 285.  
 Jameson, H. L., 377.  
 Janssen, Mgr., 345.  
 Janssens, chiasmatype theory, 209.  
 Jenkins, F., 135, 138, 145, 148; and Darwinism, 132.  
 Jenkinson, W. J., 243.  
 Jennings, H. S., and Lamarckism, 252, 273, 274; on pure lines, 190.  
 Jensen, H. W., on gene theory, 244.  
 Johannsen, W., criticism of gene theory, 245-246; pure line theory, 189-190.  
 Joluston, O., and back mutations, 313.  
 Jollo, V., 273, 274, 303, 307; and *dauer-modification*, 243.  
 Jordan, D. S., 150.  
 Jordanons, 282.  
 Jorgensen, C. A., chromosomes in *Solanum*, 191.  
 Jussieu, A. de, and plant classification, 42.  
 Just, E. E., 244, 309.  
*Kallina*, 124.  
 Kammrer, P., 254, 368; evidence for Lamarckism, 256-258.  
 Kane, J., 377.  
 Kangaroo, laryngeal structures, 124.  
 Kant, I., 38, 51, 53-58, 61, 68, 81, 104, 117; and discarding of teleology, 54, 57; and "understanding", 55; definition of organism, 54; on evolution and genetic relationship, 56.  
 Karpechenko, G. D., on *Raphanobrassica*, 218.  
 Karyotype, 193.  
 Kassowitz, M., and Darwinism, 121.  
 Keck, D. D., 332.  
 Kellogg, V. L., 119, 121, 139, 146, 150, 170, 253, 368.  
 Kepler, 60.  
*Khepera*, 10.  
 Killouh, D. T., and mutations, 306.  
 Kirkpatrick, A. F., 328.  
 Knox, R., 86.  
 Koken, E., 169.  
 Kölliker, A. von, 116, 152; and Darwinism, 121; and mutation theory, 172.  
 Külreuter, 64, 182.  
 Korschinsky, H., and Darwinism, 122; and heterogenesis, 173; and orthogenesis, 167.  
 Krause, E., 63; and Darwinism, 121.



- Labyrinthodon, 125.  
 Lamarck, Jean Baptiste de, 4, 38, 43, 46, 51, 61, 62, 63, 79, 81, 87, 88, 98, 99, 109, 123, 137, 151, 155, 158, 181, 254, 255, 280; and Buffon, 48; and evolution, 68-78, 91; and mechanism, 72-73; classification compared with Linnaeus, 71; classification of animals, 353-360; creation of philosophical system of zoology, 69; definition of species, 69-70; laws of use and disuse, 75, 76; principle of affinities, 70-71.  
 Lamarckian principle, 162.  
 Lamarckism, 68-78, 111, 137, 151, 156, 160-166, 167, 181, 253, *see also* Neo-Lamarckism; and Charles Darwin, 138-140; and Erasmus Darwin, 65, 67, 68; experiments on, 253-274, 368-370; interpretative difficulties, 163; rejected by Owen, 96; the New, replacing natural selection, 50-51.  
 Lamprecht, H., 229.  
 Lang, J. M. S., 332.  
 Lange, F. A., and Darwinism, 121.  
 Lankester, Ray, 95, 140.  
 Laplace, P. S. de, 60, 80.  
 Lashley, K., on pure lines, 190.  
 Lavoisier, A. L., 60.  
 Law, in organic world, 169; of the migration of organisms, Wagner's, 146-147.  
 Lead acetate and mutations, 298.  
 Learning, inherited facility for, in rats, 261-271.  
 Leeuwenhoek, A. von, 60, 100.  
 Lefevre, J., 347.  
*Legend of the Creation*, Chinese, 10.  
 L'Heritier, P., on *Drosophila*, 331.  
 Leibniz, 38, 45, 172; and evolution, 53.  
 Lemcke, H., and melanism in moths, 301, 302.  
 Lemoine, P., 347.  
*Lepidoptera*, 299.  
 Lethal, autosomal chromosomal, 375-377.  
*Leuciscus erythrophthalmus*, 329, 330.  
 Levit, B. G., 239.  
 Lewis, G. N., and mutations, 308.  
 Lewinsky, G. A., and idiograms in related forms, 193.  
 Leydig, F., 122.  
 Life, origin of, and evolution, 343, 344.  
*Liliaceae*, 39.  
 Lillie, F. R., 241.  
 Lindgren, D. L., on Scale Insects, 328.  
 Lindsay, A. D., 54, 57.  
 Linkage, 194; definition of, 198; additive theorem of, 201.  
 Linnean Society, Centenary Meeting of, 107.  
 Linnaeus, Carl, 31, 42, 43, 57, 71; systems of classification, 39-41.  
 Linneon, 281, 282.  
 Lithium carbonate and mutations, 298.  
 Locy, W. A., 30.  
 Loeb, J., 136, 243; prophecy, 213.  
 Lotsy, J. P., hybridization theory, 280-282.  
 Lowes, F. E., 25.  
 Lucretius, 34, 63.  
*Lusus naturae*, 97.  
 Lutz, A. M., 216.  
 Lutz, F. E., 377.  
*Lycopodiales*, 282.  
 Lyell, Sir Charles, 80, 81, 98, 107, 115, 119.  
*Lymantria monacha* L., 289, 368.  
 Lynch, R. S., 273.  
 McAtee, W. L., 339.  
 MacBride, E. W., and Haldane, 255, 260; and Harrison, 260; and Lamarckism, 255; on Kammerer's work, 257; on Metchnikov, 370; on natural selection, 106, 339.  
 McClintock, B., cytology of *Zea*, 209, 229, 233.  
 McClung, C. E., and sex chromosomes, 202.  
 McCullagh, D., and idiograms in related forms, 193.  
 MacDougall, M. S., and mutations, 307.  
 McDougall, W., Lamarckian experiment, 261-271.  
 Mackay, W., differences between affinity and analogy, 93.  
 McKay, J. W., and mutations, 306.  
 McMurtie, H., translation of Cuvier's *Régne Animal*, 89.  
*Macrauchenia*, 126.  
 Macro-evolution, Goldschmidt on, 288-295.  
 Maillet, de, 38, 44, 61, 63.  
 Maize, *see Zea mays*.  
 Malpighi, M., 60, 100.  
 Malthus, T. R., 63; essay on Population, 107.  
*Mammalia*, 43, 71, 89, 95, 125, 359; aquatic, 254; reproduction by eggs, 101.

- Mammals, *see* *Mammalia*.  
 Man, evolution of, according to E. Darwin, 65.  
*Manlis religiosa*, 335-336.  
 Manwaring, W. H., 273.  
 Maps, chromosome, in *Drosophila*, 201, 208; in maize, 201; in pea, 201; method of obtaining, 365-368.  
 Marchant, J., 108, 122, 123.  
 Maritain, J., 349.  
 Marsden-Jones, E. M., 332, 333.  
 Mastodons, 278.  
*Materia prima*, 352.  
 Materialism and evolution, 51, 57, 349.  
 Matthews, P., 109.  
*Matthiola incana*, 229, 233.  
 Mattoon, E. W., on pure lines, 190.  
 Maupertius, P. L. M. de, 44.  
 Mechanico-physiological theory of evolution, C. von Nägeli's, 166-167.  
 Mechanism, 52, 55, 58, 72, 262, 346, 349.  
*Medusae*, 70.  
 Meiosis, Darlington definition of, 188; pairing of chromosomes in, 207.  
 Melander, A. L., 327.  
 Melanism, induction of, in moths, 299-301.  
 Meldola, Prof., 83.  
 Memory, larval and Lamarckian experiments, 260-261.  
 Mendel, G., 8, 138, 171, 178, 181, 196, 197, 237, 242, 281, 348.  
 Mendelian experiment, factorial account of, 360-362.  
 Mendelian expectations, deviations from, 193-196.  
 Mendelian factors, as entities, 198.  
 Mendelism, 102, 182-188, 245; basic postulates of, 185-186; cytological explanation of, 186-188; in moths, 300; particulate nature of, 186.  
 Merz, T., 87, 90, 91.  
 Messenger, E. C., 4, 6, 129, 131, 345.  
 Metalnikov, S., on *Galleria*, 370.  
*Metamorphosis of Plants*, Goethe's, 81.  
 Metaphase, stage in nuclear division, 192.  
 Methyl bromide, 328.  
*Metrioptera brachyptera*, 229.  
 Methylene blue, 298.  
 Mice, and selection, 377; epistasis in, 196.  
 Michaelis, P., 243.  
 Micro-evolution, 212; Goldschmidt on, 288-295.  
 Milicos, 11, 14.  
 Mill, J. S., and Darwinism, 119.  
 Mimicry, 333-339; and Darwinism, 124.  
 Mimics, Batesian, 334, 338; Mullerian, 334, 338.  
*Mirabilis jalapa*, genetics of, 194.  
 Mitosis, 187, 192.  
 Mivart, St. G., 120, 122, 123, 138, 151, 173, 287; and existence of internal force, 127; criticisms of Darwinism, 115, 123-128; on evolution and religion, 128-132; on origin of man, 131-132.  
 Mizellens, Nägeli's, 167.  
 Modern period of evolution, 181-341.  
 Modifications, 214; factors producing, 215.  
*Moeritherium Andrewsii*, 278.  
 Mohammedanism, 35.  
 Mohl, von, 101.  
*Mollusca*, 43, 70, 76, 88, 359.  
 Monads, Leibnez', 45.  
*Monas*, 358.  
 Monocotyledons, 39, 42.  
 Montgomery, 188, 201.  
 Morgan, Lloyd, 140, 167; organic selection, 151-152.  
 Morgan, T. H., 45, 47, 204, 206, 209, 223, 238, 239, 244, 246, 248, 296, 298, 315, 348, 371; and chromosome theory, 197; and Darwinism, 122; early supporter of mutation theory, 176.  
 Morley, W., 347.  
 Mott-Smith, L. M., on mutations, 308.  
 Mouse, and mutations, 306.  
*Mucor*, mutations in, 304.  
 Muller, H. J., and linkage in *Drosophila*, 198; measurement of mutation rate, 371-377; on mutations in *Drosophila*, 138, 226, 227, 230, 302, 303, 304, 305, 306, 308, 309, 313, 348; on salivary gland chromosomes, 208.  
 Multiple factor theory, 195-196.  
 Müntzing, A., 229; and inversions, 233; chromosome numbers in *Potentilla*, 191; synthesis of *Galeopsis tetrahit*, 219.  
 Murphy, J. J., 125, 173.  
 Murray, R. H., 107.  
 Mutation theory, of evolution, 170-178; evolution by divergent, 285-288.  
 Mutations, 171, 172; and evolution, 288-295, 312-319; and physiology, 297; and selection, 296-341; buffering of, 238; chromosome, in *Datura*, 224-225; definition of, 178; deleterious, or lethal, 309, 312, 315, 318, 321; detection of non-visible, 375-376;

- gene, or point, 310-319; in *Drosophila*, 227, 228; induction of, 296-310; induction by chemicals, 298-302; induction by heat, 302-304; induction by radiations, 304-310; Muller's technique for measuring rate of, 371-377; nature of, 310, 311; of *Oenothera Lamarckiana*, 174-178; of sperms and eggs, in *Drosophila*, 309; physiological, 314, 316; random occurrence of, 313, 314; rate and temperature, 303; reverse, in *Drosophila*, 313; systematic, 294; variation of viability in, 316.
- Mutationsrichtung*, 278.
- Nabours, R., 314.
- Nadson, G. A., and mutations in *Mucor*, 304.
- Nägeli, C. von, 45, 102, 153, 167, 168, 275; and Darwinism, 121; interpretation of evolution, 166.
- Naturalists, The, 38-44.
- Naturalists, The Speculative, *see* Philosophers, Speculative.
- Nature, the two aspects of, 57-58.
- Naudin, M. C., 173; anticipation of natural selection, 109.
- Navaschin, M., and the idiogram, 193; on *Crepis*, 63, 64.
- Neb-er-Tcher*, 10, 11.
- Neo-Darwinism, 137, 138-140, 318; and Goldschmidt, 288-295; and Weismann, 159-160; modern, 296-341; position of natural selection in, 319-341; reconciliation with mutation theory, 238.
- Neo-Lamarckism, 73, 137, 138-140, 160-166, 251-274, 320; a legitimate theory of evolution, 162; and orthogenesis, 162, 168, 275; and Weismann, 159-160; modern evidence in support of, 253-274; modern evidence in multicellular organisms, 368-370; modern evidence in unicellular organisms, 273-274.
- Newman, H. H., 13, 25, 30, 253, 345.
- Newport, G., and fertilization, 152.
- Newton, Sir Isaac, 48, 55, 60, 80.
- Newton, W. C. F., on amphidiploids, 218.
- New Zealand, flora of, 283-284.
- Nicotiana glauca*, a new "species", 218.
- Nicotiana paniculata*, 64.
- Nicotiana rustica*, 64.
- Nicotiana tabacum* x *N. glutinosa* hybrid, 218.
- Nicotiana tabacum* x *N. sylvestris* hybrid, 222.
- Nilsson-Ehle, H., 347; multiple factor theory, 195.
- Noethling, W., and mutations, 307.
- Nominalism, 59-60.
- Nomogenesis*, Berg's, 117, 169-170.
- Nordenskiöld, G., 11, 13, 17, 25, 30, 35, 39, 41, 42, 49, 101.
- Normandy pigs, 125.
- Nu*, 10.
- Obscure period of evolution, 8, 9-11, 342.
- Occam, William of, 59.
- Oenothera*, 137, 229; mutations in, 175-176; translocation in, 229, 230.
- Oenothera gigas*, 216.
- Oenothera Lamarckiana*, 175-177, 216; as a hybrid, 176.
- Oenothera suaveolens*, 40.
- O'Gorman, P. W., 347.
- Oken, L., 38, 44, 63, 81, 92, 101; and the *Urschleim*, 46.
- Olsen, A. R., 306.
- Ontogeny, 275, 276.
- Oporabia autumnata*, 289, 340; evolution of, 325-327.
- Organicists, 250.
- Organismal interpretation of living things, 248-250.
- Origin of new characters, palaeontologic, 276-277.
- Origin of Species*, C. Darwin's, 52, 61, 79, 80, 93, 95, 99, 104, 105, 106, 109, 110, 111, 114, 115, 116, 119, 121, 122, 123, 129, 131, 132, 135, 139, 144, 164.
- Origin of things, Empedocles', 15-16.
- Orthogenesis, 166-170, 274-280; as an expression of order not chance, 169; as pre-determined evolution, 170; force behind, 168; Osborn's aristogenetic theory of, 274-280; Weismann's ideas of, 159.
- Orthoselection, 167-168.
- Osborn, H. F., 6, 7, 13, 25, 26, 27, 30, 44, 48, 53, 61, 66, 80, 86, 88, 140, 164, 277; on organic selection, 151; the unknown factor, 252, 275; theory of aristogenesis or biomechanical evolution, 274-280.
- Ostergren, G., 233.

- Ostracoderm*, 353.  
 Ostrich, callosities of, 254.  
 O'Toole, G. B., 347.  
 Overproduction and Darwin, 112-113.  
 Owen, J., 50.  
 Owen, R., 81, 87, 92-97, 99, 173, 287;  
 acceptance of evolution or trans-  
 mutation, 95, 96; and principle of  
 homology, 92-93; and the archetype,  
 94; derivation hypothesis, 97; re-  
 jection of special creationism, 95;  
 rejection of Lamarckism and Dar-  
 winism, 96.  
 Packard, A. S., 68, 69, 78, 139, 165, 252;  
 and Darwinism, 121.  
*Paeonia*, 229.  
 Painter, T. S., on *Drosophila* salivary  
 glands, 208.  
*Palaeomastodon intermedius*, 279.  
 Palaeontology, 97-100; and aristogenesis,  
 274-280; foundation of evolutionary  
 theory, 99; growth of, 97-98.  
*Palaeoplotherium*, 95.  
*Palaeotherium*, 95.  
 Pangensis, Darwin's theory of, 152.  
 Paraguay cattle, 171.  
 Parallel induction, Weismann's theory  
 of, 157, 158.  
*Parametium*, Lamarckian experiments on,  
 273.  
*Paris quadrifolia*, inversion in, 234.  
 Parmenides, 15.  
 Parthenogenesis, 45, 354.  
 "Passing away", 347, 351.  
 Patterson, J. T., and back mutations, 313.  
 Payne, F., on *Drosophila*, 254.  
 Pea, sweet, Bateson on, 194.  
 Peacock, A. D., on Sawfly, 138.  
 Pearl, R., and logical requirements of  
 natural selection, 321.  
 Pearson, Hesketh, 62.  
 Pearson, K., 377.  
*Pedicellariae*, of echinoderms, 124.  
 Pellew, C., 219.  
 Penguin, Galapagos, 335.  
*Pentstemon azureus*, 221.  
*Pentstemon lactus*, 221.  
*Pentstemon neotericus*, a natural amphidi-  
 ploid, 221.  
 Pentavalents, 229.  
 Perfection, Hunter's idea of, 50.  
 Phanerogams, 40.  
 Phenotype, 361.  
 Philipov, G. S., and mutations in *Mucor*,  
 304.  
*Philosamia Cynthia*, 368; selective elimina-  
 tion in, 324-325.  
*Philosophia Botanica*, Linnaeus', 40, 41.  
*Philosophie Zoologique*, Lamarck's, 43, 66,  
 69, 80, 91, 98.  
 Philosophers, the Speculative, 38, 44-47,  
 51, 61.  
 Philosophers, the Natural, 38, 51-58, 61.  
 Philosophers, Chinese, 9.  
 Philosophy, Ancient Greek, 11-21; and  
 evolution, 345, 347; Aristotelian,  
 18-21, 29, 33, 36; central problem  
 of, 44; Chinese, 9-11; evolution a,  
 342; Ionian School of, 12-18;  
 modern, 51-62, 72, 104, 105, 128,  
 129, 130, 262, 346, 349; revolt  
 against mediaeval, 59; scholastic  
 (and Thomist), 20, 34, 35, 44, 52,  
 345, 346; scholastic, confusion with  
 scholastic theology, 36; speculative,  
 44-47.  
 Philip, J., 201, 209, 216, 219, 229, 232.  
*Phionia Osborni*, 279.  
*Phratora vitellinae*, 369.  
*Pieris brassicae*, 369-370.  
*Pieris napi*, 370.  
*Pisces*, 46.  
*Phleum nodosum*, 333.  
*Phleum pratense*, 33.  
 Phylogeny, 276.  
*Phycomyces Blakesleeanae*, mutations in, 304.  
*Physcomitrium*, 219.  
*Physica*, Aristotle's, 18, 20, 21, 25, 26, 27,  
 351, 352.  
 Physiology, development of, 81.  
 Pictet, A., 368.  
*Pisum sativum*, Mendel's work on, 183-186.  
*Planorbis*, 352, 368.  
*Plantago major*, 333.  
 Plants, classification of, 38-42.  
 Plate, L., 139, 144.  
 Platt, A., 357.  
 Pleiotropy, 196.  
 Pliny, 34, 37.  
 Plough, H. H., and mutations, 303.  
 Plunkett, C. R., on melanism in moths,  
 301.  
*Plutella*, 368.  
*Podostemaceae*, 285.  
*Poem of Nature*, Empedocles', 15, 25.  
 Polimeni, E., 347.  
 Polyploidy, 191, 192; and evolution, 216-  
 220; complex, as a closed system,  
 223; Stebbins' review, 222-223.

- Polyper*, 70, 358.  
 Polysomes, 192, 292; in plants, 224.  
*Pontania salicis*, Harrison's work on habits of, 258-261.  
 Poole, C. F., 220.  
 Popham, E. T., on *Arctocoris*, 329-331.  
 Population, genetic composition of, 188, 189, 190.  
 Potentiality of Creation, 11.  
*Potentilla*, chromosome numbers in, 191.  
 Poulson, D. F., 227.  
 Poulton, Sir Edward, 105, 377; and Prichard, 83-84.  
 Preformation, 45.  
 Presence-absence hypothesis of Bateson and Punnett, 197, 239, 313.  
 Prevost, 152.  
 Preyer, W., and Darwinism, 121.  
 Prichard, J. C., 83-86.  
 Priestley, J., 60.  
*Primula floribunda*, 219.  
*Primula kewensis*, 219; behaviour of chromosomes in, 220.  
*Primula verticillata*, 219.  
 Principles, adaptive bio-mechanical, 275, 277; vital, 94.  
 Progress, philosophic idea of, 346.  
 Prokofjeva, A., 208.  
*Proteus*, 76; *anguinus*, Kammerer on, 254.  
*Protista*, 101, 243.  
 Protoplasm, name given by Perkinje, 101.  
*Protozoa*, 273.  
 Przibram, H., 253.  
 Punnet, R. C., 198; and presence-absence hypothesis, 197; on sweet pea, 194.  
 Pure line theory, 189-190.  
*Purifications*, 'Empedocles', 15-16.  
 Purkinje, J., 101.  
 Purpose, in nature, 54, 55.  
 Pycraft, 23.  
*Pygaera*, hybrids, 207, 218.  
*Pyrrhocoris apterus*, 202.  
  
 Quadrivalents, in *Avena* and *Triticum*, 220.  
*Quadrumania*, 89.  
 Quatrefages, J. L. A. de, 44; and Darwinism, 122.  
 Quayle, H. J., on Scale Insects, 327-329.  
 Quinine, and mutations, 298.  
  
 Rabaud, E., 245.  
 Races, 289, 290.  
  
*Radiata*, 43, 70, 88, 358.  
*Radiomorphose*, 304.  
 Radl, E., 77, 111, 116, 121, 166.  
*Rambler*, The, 129.  
 Ramsbottom, J., 41.  
 Randolph, L. F., 221.  
*Raphanobrassica*, a new genus, 218.  
*Rassenkreis*, 289, 290, 291.  
 Rates, mutation, *see* Mutation.  
 Ratios, dihybrid, 362; monohybrid, 360-361; monohybrid, statistical analysis of, 363; sex, statistical analysis of, 364; simple Mendelian, 184.  
 Rats, McDougall's work with, 261-271.  
 Rattlesnake, 124.  
 Ray, John, classification of plants, 39, 43.  
 Recapitulation theory, explained by orthogenesis, 170.  
 Recessiveness, genetic, 184.  
 Rectigradations, 276.  
 Relationship, genetic, Kant's recognition of, 56-57.  
 Renaissance, the, 37, 59, 60, 348.  
 Renouf, L. P. W., 238.  
 Repeats, chromosome, 228.  
 Reproduction, according to Aristotle, 353-354; sexual, essence of, 152; sexual, Mendelian, 360.  
 Reptiles, 357, 359.  
 Resemblance, protective, 333-339.  
 Rhine, J. B., 261.  
 Rhoades, M. M., on maize, 297.  
 Richards, O. W., 315, 316, 370; and Lamarckism, 253; and natural selection, 322, 340.  
 Richerand, 72.  
 Rifenburgh, S. A., and mutations, 307.  
 Right whale, rudimentary teeth in jaws of, 75.  
 Rivinus, 39.  
 Robbins, R. B., on pure lines, 190.  
 Roberts, Fraser, 206.  
 Robinet, 46.  
 Robson, G. C., 315, 316, 378; and Lamarckism, 253; and natural selection, 322, 340.  
 Rolle, F., and Darwinism, 121.  
 Romanes, G. J., 109, 116, 119, 139, 140, 150, 156, 160, 253; and physiological selection, 148-149.  
*Rosa canina*, 40.  
*Rosa pimpinellifolia*, 219.  
*Rosa tomentosa*, 219.  
*Rosa Wilsonii*, 219.  
 Rosenberg, O., idiograms in related forms, 193.

- Rostovtsov, J. N., trans. of Berg's *Nomogenesis*, 170.
- Roux, W., "battle of the parts", 150, 157.
- Rückert, J., 188.
- Rule, linear proportionality, in mutations 309; Van't Hoff and mutations, 304.
- Russell, B., 53.
- Russell, E. S., criticism of gene theory, 248-250; organismal theory, 249-250.
- Sachs, J. von, and Darwinism, 121.
- Saint-Hilaire, Geoffrey, 8, 43, 51, 86, 89, 91, 165; and evolution by differentiation, 287; debate with Cuvier, 92; unity of organic composition, 90.
- Saint Hilaire, Isidore, 91.
- Saissetia oleae*, 328.
- Salisbury, Marquis of, Presidential address to B.A., 117.
- Salamander atra*, 257, 258.
- Salamander maculosa*, Kammerer on, 256, 257, 258.
- Salix Andersoniana*, 259, 260, 261.
- Salix phylicifolia*, 259, 260.
- Salix purpurea*, 259.
- Salix rubra*, 259, 260, 261.
- Saltations, *see* Mutations.
- Sansome, F. W., 201, 209, 216, 219, 229.
- Sarcode, contents of Protistan cells, 101.
- Satina, S., 229.
- Saunders, Carr., 369.
- Sawfly, *see* *Pontania*.
- Schelling, F. W., 81.
- Schleiden, M. J., 47, 137, 187; formulation of cell theory, 101-103.
- Schmidt, O., and Goethe, 82; fertilization in plants, 152; on Darwinism, 121.
- Scholasticism, period of, 34, 36, 52, 59.
- Scholastics, the, 35, 44, 345, 346.
- Schroder, C., on *Graciliera*, 368.
- Schultze, M., protoplasm as physical basis of life, 101.
- Schwann, Th., and cell theory, *see* Schleiden.
- Scientism, 349.
- Scolex, 24, 31, 355.
- Scott, W., 169.
- Scotus, Duns, 59.
- Sea-cucumbers, 353, 356.
- Sea-urchins, 353, 356.
- Seal, 354.
- Secondary sex characters, 144-145.
- Sedge warblers, 336.
- Sedgwick, W. T., 87, 101, 122.
- Seebohm, H., criticism of Romanes, 149, 150.
- Segmental interchange, in chromosomes, 225, 228-233.
- Selachii*, 354, 357.
- Selection, and Lamarckian factor, 160-163; and pure lines, 189-190; germinal, Weismann's theory of, 157; germinal, and lethal genes, 306; in Lotsy's theory, 282; in self-pollinated plants, 189; organic or coincident, 151-152, 261;
- Selection, natural, a metaphysical expression, 114; and acridians, 337; and *Arctocoris*, 329-331; and Aristotle, 26-28; and Buffon, 49; and *Colias philodice*, 336-337; and evolution, 339-341; and Empedocles, 16; and *Gambusia*, 334-335; and *Mantis*, 335-336; and modern Neo-Darwinism, 319-341; and *Oporabia*, 325-327; and *Philosamia*, 324-325; and scale insects, 327-329; anticipated by Prichard, 85; anti-teleological character of, 128; appeal to commonsense, 135; comparison of Darwin's and Wallace's theories of, 140-142; complete demonstration wanting, 321; criticism of, 285, 287; direct observational evidence for, 322-331; early evidence for, 377; enunciation by Darwin and Wallace, 107-108, 111; indirect observational evidence for, 331-339; modern evidence for, 322-341; Pearl's logical requirements of, 321; theories, replacing, 160-178; theories subsidiary to, 138, 143-160; theory, justification of, 341.
- Selection, sexual, Darwin's theory of, 143-145.
- Selectionists, mathematical, 290.
- Selenia bilunaria*, induction of melanism in, 289, 300-302.
- Semon, R., 253.
- Serebrovsky, A. S., 239.
- Serpents, 76, 357.
- Settles, F., 230.
- Seward, A.C., and Prichard, 83, 109.
- Sex, chromosome mechanism, 202-207; in flowers, 40, 82; ratio, 202.
- Sexton, E. W., on wild population of *Gammarus*, 311.
- Shapiro, H., 341.
- Sharp, L. W., 211; and cell theory, 102.

- Shaw, G. B., 62.  
 Shepherd's purse, genetics of, 195.  
 Shimotomai, U., chromosome numbers in *Potentilla*, 191.  
 Short, Rendle, 347.  
 Shull, G. H., 195.  
*Silene cucubalus*, 333.  
*Silene maritima*, 333.  
 Silfast, J., 369.  
 Silkworm, mulberry, 368; mutations in, 306.  
*Simonephalus vetulus*, 368.  
 Simonet, M., 191.  
 Singer, C., 5, 25, 35, 48, 66, 351.  
 Sinnott, E. W., 215.  
 Sitko, P., 297.  
 Skin, inheritance of porcupine, 206.  
 Skovsted, A., 219.  
 Sladden, D. E., on *Carausius*, 271-272.  
 Slaley, R. W., 10.  
 Smith, E., on serology, 369.  
 Smith, N. Kemp, 54.  
 Smith, W., 98.  
 Snakes, *see* Serpents.  
 Social Democrats, 121.  
 Socolov, D., 234, 293.  
*Solanum*, chromosome numbers in, 191.  
 Sonneborn, T. M., 273; criticism of McDougall, 267.  
 Sophists, the, 17.  
 Souvay, Very Rev. Dr. C. L., 4.  
*Spalax*, 76.  
 Spallanzani, discovery of spermatozoa, 152.  
 Sparrows, English, 377.  
*Spartina alterniflora*, 221.  
*Spartina stricta*, 221.  
*Spartina Townshendi*, a natural amphidiploid, 221.  
 Special Creationism, *see* Creationism.  
 Species, confusion with individuals, 116; Cuvier's definition of, 88; different meanings of, 289; elementary, 175; endemic, 283; geographic variation of, 291; geological history of, 291; immutability of, 30, 32, 43, 48, 85, 354; incipient, 124, 290; Lamarck's definition of, 69-70; "new", 222, 349; Prichard's views of, 85; recognition of mutability of, 57.  
*Species Plantarum*, Linnaeus', 40.  
 Speculative period of evolution, 7, 37-58, 342.  
 Spencer, H., 61, 140, 156, 252; as a Lamarckian, 164; definition of evolution, 104-105; influence on evolutionary thought, 105; physiological units, 241.  
 Spencer, W. P., on *Drosophila*, 314, 332.  
 Sponges, 32, 353, 356.  
*Sporozoa*, Dobell on, 246-248.  
 Sprague, G. F., and mutations, 307.  
 Squirrels, 233.  
 Stadler, L. J., 223, 298, 302, 306, 307, 311, 314.  
 Stancati, M. F., and mutations, 306.  
 Standfuss, M., 368.  
 Stanford, E., 146.  
 Stebbins, G. L., 222.  
 Stedman, 240.  
 Stein, E., mutations in *Antirrhinum*, 304.  
 Steinman, G., and Darwinism, 122.  
 Stensen, Bishop N., on fossils, 97.  
 Stereoplasm, Nägeli's, 168.  
 Stern, C., on *Drosophila*, 209, 229.  
 Stevens, D.M., 203.  
 Stewart, C., 81.  
 Stieve, H., 245.  
 Stocks, J. L., 18.  
 Stone Age, the, 7.  
 Strasburger, E., on fertilization, 187.  
*Streptococcus haemolyticus*, 331.  
 Stroer, W. F. H., 242.  
 Strychnine and mutations, 298.  
 Stubbe, H., 299, 307.  
 Stubboid gene in *Drosophila*, 319.  
 Sturtevant, H., on *Drosophila*, 228, 233, 244, 293, 298, 315; and selection, 318.  
 Suarez, F., 120, 131.  
 Sub-genes, 239.  
 Sugars, and mutations, 298.  
*Summa contra Gentiles*, St. Thomas's, 36.  
*Summa Theologica*, St. Thomas's, 129.  
 Sumner, F. B., and Lamarckism, 252; on *Gambusia*, 334-335.  
 Survival, mutations and selective, 316-318.  
 Sutton, W. S., 178, 188, 201; and chromosomes, 138.  
 Sveshnikova, I., 207.  
 Sweet pea, genetics of, 194.  
 System, chromosome reaction, 293-295; genetic and cytogenetic evolutionary, 213; of affinity, 70-71.  
*System Natura*, Linnaeus', 40, 41.  
 Systematics, and taxonomy, 81.  
 Tahara, M., chromosome numbers in *chrysanthemum*, 191.  
 Taliaferro, W. H., 273.

- Tan, C. C., 234.  
*Tao, Taoists*, 9, 10.  
 Taxonomy, and systematics, 81.  
 Taylor, A. E., 25.  
 Taylor, W. R., and idiograms in related forms, 193.  
 Technic of Nature, 56.  
 Teeth, rudimentary, in whale foetus, 75.  
 Teissier, G., 331.  
 Teleology, 54, 55, 57, 221, 345, 348, 349.  
*Tellamed*, de Maillet's, 44.  
 Teleosteans, bony or scaly fishes, 357.  
*Temple of Nature*, Erasmus Darwin's, 63, 64, 65.  
*Tephrosia bistortata*, induction of melanism in, 300.  
 Tertiary age, 291.  
*Testacea*, 32, 353, 356.  
 Tetraivalents (and quadrivalents), 208, 223, 229.  
 Thales, the Ionian, 11, 12.  
 Theophrastus, 33, 34.  
*Theorie Generationis*, C. F. Wolff's, 100.  
 Theory, age and area, 283-285; Butler's memory; 166; cell, *see* Cell theory; chromosome, *see* Chromosome theory; Darwinian, *see* Darwinism and Neo-Darwinism; Darwin's pangenesis, 152, 241; epigenetic, 45; evolution, *see* Evolution theory; gene, *see* Gene theory; genomeric, 239; Goethe's unity of type, 82; Janssen's chiasmotype, 209; multiple factor, 195; mutation (heterogenesis), 170-178, 288-295, 296-319; of archaesthetism, 169; of catastrophism, *see* Catastrophism; of evolution by differentiation, 285-288; of indirect chromosome binding, 217-218; of special creation, *see* Creation; organismal, 249-250; preformation, 45; presence-absence, 197, 239, 313.  
 St. Thomas, *see* Aquinas.  
 Thomists, 352.  
 Thompson, E., 377.  
 Thompson, W. R., 27.  
 Thomsen, M., on melanism in moths, 301-302.  
 Thomson, J. A., 153, 160, 253.  
 Thomson, M. R., 153.  
 Thorpe, W. H., 268.  
 Thought, Ancient Chinese, Babylonian, Egyptian, 9-11.  
 Time of experimentation, 8.  
 Timofeeff-Ressovsky, N. W., 296, 297, 304, 307, 309, 310, 313, 315, 316, 319, 332, 348; and wild populations of *Drosophila*, 311; interaction of genes, 237.  
 Tiniakov, G. G., 293.  
*Titanotheres*, 168; as orthogenetic series, 274.  
 Tobacco, mutations in, 306.  
 Todd, C., on *Streptococcus*, 331.  
 Tomato, trisomics in, 224.  
 Torrey, H. B., 25, 26, 30, 33.  
 Tournefort, and plant classification, 38, 39.  
 Tower, W. L., 368.  
*Tradescantia*, 233.  
*Traite de l'Homme*, Descartes', 52.  
 Transformation, immediately after Lamarck, 81-86.  
*Transformisme*, 295.  
 Translocation, chromosome, 225, 228-233, 294.  
 Transplant experiment, of Marsden-Jones and Turrill, *et al*, 332-333.  
 Treviranus, R., introduction of word "biology", 72, 80.  
 Trilobites, 344.  
*Triticum*, natural groups of, 191.  
*Triticum durum*, 218.  
*Triticum vulgare*, 220.  
*Trimeropteris*, unequal chromosomes in, 207.  
 Triploids, pairing of chromosomes, 208.  
*Triplophodon Cooperi*, 279.  
*Triplophodon chinjiensis*, 279.  
*Triplophodon macrognathus*, 278, 279.  
*Triplophodon palaeindicus*, 279.  
 Trivalents, 229.  
 Tschermak, E., 8, 102, 138, 182; synthesis of *Aegilotriticum*, 218.  
 Tschetverikov, S. S., on wild populations of *Drosophila*, 311.  
*Tubifex*, 368.  
*Tulipa* species, 229, 233.  
*Turbinata*, 353, 356.  
 Turesson, G., and ecotypes, 332.  
 Turkeys, 337.  
 Turning point, in evolutionary theory, 181-211.  
 Turrill, W. B., 332, 333.  
 Tyler, H. W., 87, 101.  
 Ultra-violet light, and production of mutations, 307.  
 Understanding, Kant's special meaning of, 55.  
 Unger, F., 102.



- Ungulicula*, 95.  
 Uniformity, principle of, and gene theory, 243.  
 Unity of type, Goethe's theory of, 82.  
 Univalves, 353, 356.  
 Upcott, M., 229, 233.  
*Urschleim*, of Oken, 46, 101.  
  
 Variations, and Darwin, 111-112; bud, 215; caused by chromosomal changes, 215; discontinuous, 171, 174; genotypic, 189; or autogenous variations, in general, 214-216; phenotypic, 189.  
*Vanessa urticae*, 368, 377.  
*Vermes* (worms), 43, 71, 358.  
*Vertebrata*, 43, 71, 88, 124.  
*Vesalius*, 60.  
*Vespa vulgaris*, 377.  
*Vibrio*, 370.  
*Viola*, polymorphic species, 177.  
 Vilmorin, R. de, 191.  
 Virchow, R., 47, 187; aphorism of, 102; and Darwinism, 121.  
 Viruses, 344.  
*Vision of Hermes*, 11.  
 Vitalism, 51.  
 Vogt, C., and Darwinism, 121.  
 Vries, H. de, 8, 40, 103, 137, 138, 280; and Darwinism, 122; and mutation theory, 171-172, 174-178.  
  
 Waagen, W., 276; and mutation theory, 172.  
 Waddington, C. H., 183, 216, 243; and the additive theorem, 201.  
 Wagner, M., and Darwinism, 122; geographical isolation, 145, 146-147, 148, 165, 280.  
 Wallace, A. R., 61, 68, 105, 111, 117, 119, 122, 123, 139, 146, 173; and Darwin, 140-143; enunciation of theory of natural selection, 107-108; letters, 122.  
 Walther, H., and mutations in moths, 302.  
 Warmke, H. E., 296.  
 Wasps, mutations in parasitic, 306.  
 Watkins, A. E., on wheat cytology, 191.  
 Watson, D. M. S., 106.  
 Watson, E. L. Grant, 347.  
 Watt, J., anticipation of natural selection, 109.  
 Watts, W. W., 97.  
  
 Weismann, A., 61, 102, 105, 111, 118, 121, 137, 139, 140, 187, 275; anticipated by Prichard, 83; opponent of Lamarckism, 156.  
 Weismannism, 152-160, 241.  
 Weldon, W. E. B., 377.  
 Wells, W. C., and natural selection, 109.  
 Wenrich, D. H., 207.  
 Wettstein, F. von, and cytoplasmic inheritance, 243; on *Physcomitrium*, 219.  
 Whale, right., 75.  
 Wheat, multiple factors in, 195; mutations in, 306.  
 Wheeler, W. H., 260.  
 Whewell, W., 99.  
 White, M. J. D., 229.  
 Whitethroats, 336.  
 Whiting, A. R., and mutations, 306.  
 Whitman, C. D., 169.  
 Wigand, A., and Darwinism, 119.  
 Wilburforce, Bishop, 115.  
 Willis, J. C., 169; age and area theory, 283-285; and mutation theory, 312; criticism of natural selection, 285-287; theory of evolution by divergent mutations, 285-288.  
 Willow-warblers, 336.  
 Wilson, E. B., 47, 187, 188, 201, 202, 203; and cell-theory, 102.  
 Wilton Wood, 326.  
 Winchester, A. M., and back mutations, 313.  
 Windle, Sir Bertram, 19, 36.  
 Winge, O., theory of indirect chromosome binding, 217-218.  
 Winiwarter, H. de, 293.  
 Wladimirsky, A. C., 368.  
 Woghun, R. S., 328.  
 Wolff, C. F., 45, 100.  
 Wolff, G., 121, 132.  
 Woltereck, R., 368.  
 Wood, T. R., and *Drosophila*, 316.  
 Worms, *see Vermes*.  
 Wotton, Ed., 37, 43.  
 Wrens, 336.  
 Wright, S., 290, 319; on pure lines, 190; theory of dominance, 317.  
 Writers, the speculative, *see* Speculative Philosophers.  
  
 X-rays, and production of mutations, 304-310.  
 X-chromosomes, *see* Chromosomes.

Yi, *Ti-chang*, Confucius', 10.

Young, R. J., 336.

Yule, G. U., 286.

Zamenhof, S., 298.

*Zea mays*, 232; and mutation (rates), 297, 306, 314; cytology of chiasma in, 209-211; distribution of chlorophyll in, 196; translocation in, 229.

Zeleny, C., on pure lines., 190

Zimmer, K. G., and mutations, 310.

*Zingiberaceae*, 39.

Zirkle, C., and Lamarckism, 251.

Zöchler, and Darwinism, 122.

*Zoological Philosophy*, see *Philosophie Zoologique*.

Zoology, pre-Darwinian and aristogenesis, 275.

*Zoonomia*, Erasmus Darwin's, 63-67.

Zoophytes, 24.

Zygote, definition, 360.

Zygotene, stage of meiosis, 207.